An empirical and theoretical investigation of kleptoparasitic foraging behaviour in mixed-species aggregations of gulls (*Laridae*)

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Table of Contents

List of Figures and Tables 7

Overall Abstract 12

Acknowledgements 13

Part 1 – Background and literature

Chapter 0 – Preface

0.1 – Introduction 14
0.2 – Outline of the thesis 15

Chapter 1 – Social foraging theory, models of kleptoparasitism and gulls (*Laridae*) as a model system for studying kleptoparasitism

1.1 – Introduction 16
1.2 – Social Foraging Theory 16
1.3 – Models of kleptoparasitism 19
1.4 – Kleptoparasitism and gulls 22
1.5 – Summary 24

Chapter 2 – Research Aims

2.1 – Introduction 25
2.2 – Study populations and summary of the research aims 25
2.3 – Research Aim 1: To assess the role of kleptoparasitism in helping gull species invade novel environments 26
2.4 – Research Aim 2: To investigate kleptoparasitic foraging behaviour in competitively asymmetric populations 29
2.5 – Research Aim 3: An examination of the foraging behaviours used by subordinate individuals in mixed-species social groups 35
2.6 – Research Aim 4: To develop a game-theoretical kleptoparasitism model of a wild population of gulls 37
2.7 – Summary 39

Part 2 – Data and field studies

Chapter 3 – Study sites, study populations and fieldwork methods

3.1 – Introduction 41

3.2 – Study sites 41
3.3 – Study Species 44
3.4 – Measures 47
3.5 – Procedure 49
3.6 – Ethics 52
3.7 – Summary 52

Chapter 4 – Study 1: Kleptoparasitism in gulls at an urban and coastal foraging environment: An assessment of differences in the rate of kleptoparasitism across environments and the ecological predictors of kleptoparasitism

4.1 – Introduction 53
4.2 – Study rationale and predictions 53
4.3 – Analyses 54
4.4 – Results 56
4.5 – Discussion 60
4.6 – Summary 62

Chapter 5 – Study 2: Who commits kleptoparasitism, how, and against whom?

5.1 – Introduction 63
5.2 – Study rationale and predictions 63
5.3 – Analyses 65
5.4 – Results: 69

5.4.1 – Billingsgate 69
5.4.1.1 – Population composition at Billingsgate 69
5.4.1.2 – Kleptoparasitism at Billingsgate 69
5.4.1.3 – Strength of association (species & age-class) 73
5.4.1.4 – Kleptoparasite and host comparison by species age-class 74
5.4.1.5 – Kleptoparasitism by Dominant and Subordinate foragers 75

5.4.2 – Brancaster 77
5.4.2.1 – Population composition at Brancaster 77
5.4.2.2 – Kleptoparasitism at Brancaster 77
5.4.2.3 – Strength of association (species & age-class) 81
5.4.2.4 – Kleptoparasite and host comparison by species age-class 83
5.4.2.5 – Kleptoparasitism by Dominant and Subordinate foragers 85

5.5 – Discussion: 86

5.5.1 – Billingsgate 86
5.5.1.1 – Kleptoparasitism committed by GBB at Billingsgate 86
5.5.1.2 – Kleptoparasitism with GBB hosts at Billingsgate 87
5.5.1.3 – Kleptoparasitism committed by HG at Billingsgate 89
5.5.1.4 – Kleptoparasitism with HG hosts at Billingsgate 90
5.5.1.5 – Kleptoparasitism committed by BHG at Billingsgate 92
5.5.1.6 – Kleptoparasitism with BHG hosts at Billingsgate 92
5.5.1.7 – Strength of association (species and age-class) 93
5.5.1.8 – Kleptoparasite and host comparison by species age-class 95
5.5.1.9 – Kleptoparasitism by Dominant and Subordinate foragers 96

5.5.2 – Brancaster 97
5.5.2.1 – Kleptoparasitism committed by GBB at Brancaster 97
5.5.2.2 – Kleptoparasitism with GBB hosts at Brancaster 97
5.5.2.3 – Kleptoparasitism committed by HG at Brancaster 97
5.5.2.4 – Kleptoparasitism with HG hosts at Brancaster 98
5.5.2.5 – Kleptoparasitism committed by CG at Brancaster 99
5.5.2.6 – Kleptoparasitism with CG hosts at Brancaster 100
5.5.2.7 – Kleptoparasitism committed by BHG at Brancaster 100
5.5.2.8 – Kleptoparasitism with BHG hosts at Brancaster 101
5.5.2.9 – Strength of association (species and age-class) 102
5.5.2.10 – Kleptoparasite and host comparison by species age-class 103
5.5.2.11 – Kleptoparasitism by Dominant and Subordinate foragers 103

5.6 – General Discussion 104
5.7 – Summary 108

Chapter 6 – Study 3: Differences in foraging behaviour between dominant and subordinate gulls at Billingsgate

6.1 – Introduction 109
6.2 – Study rationale and predictions 109
6.3 – Analyses 110
6.4 – Results 119
6.5 – Discussion 123
6.6 – Summary 126

Part 3 - Model

Chapter 7 – Study 4: A game-theoretical model of the Billingsgate foraging population

7.1 – Introduction 127
7.2 – Study rationale and predictions 127
7.3 – Background 128

7.4 – The model 130
7.4.2 – Stage 1: Equilibrium densities of the behavioural compartments 135
7.4.3 – Stage 2: Conditions for using kleptoparasitism and defending/ resisting against kleptoparasitic attacks 137
7.4.4 – Stage 3: Candidate evolutionarily stable strategies (ESS's) 154
7.4.5 – Stage 4: Ecological conditions for ESS's 155

7.5 – Results 158
7.5.1 – Analyses and treatment of the Billingsgate foraging data 158
7.5.2 – Testing for equilibrium densities 159
7.5.3 – Comparing strategy use at Billingsgate with ecological conditions for ESS's 162

7.6 – Discussion 166
7.7 – Summary 169

Part 4 - Conclusion

Chapter 8 – General summary and concluding remarks

8.1 – General summary of the research studies 170
8.2 – Critical appraisal of the research 172
8.3 – Concluding remarks 175

References 177

Appendix A – The Hawk/ Dove Model (Maynard Smith, 1982) 184

Appendix B – Formal definitions - Nash Equilibruim (NE) and Evolutionarily Stable Strategy (ESS) 186

Appendix C – Frequency-dependent selection 190

Appendix D – Area calculations for Billingsgate and Brancaster study sites 193

Appendix E – Examples of plumages for different age categories of Herring gull 195

Appendix F – Patch Datasheet Brancaster study site 198

Appendix G – Patch Datasheet Billingsgate study site 199

Appendix H – Datasheet used for the field experiment conducted at Billingsgate 200

Appendix I – Solutions to system of dynamical equations describing equilibrium densities in the Billingsgate population 202

Appendix J – Justifying the treatment of repeatedly handled food items 208

Appendix K – Algebraic solutions for conditions for using kleptoparasitism and defending/ resisting against kleptoparasitic attacks 209

Appendix L – Tables for Study 1 Information theoretic models 217

Appendix M – Manuscript for published paper 239

Appendix N – Colour-ringed birds recorded at Billingsgate 259

List of Figures and Tables

Figures

Chapter 3:

Figure 3.1. Brancaster study site at low tide 42

Figure 3.2. Site 1 Brancaster Beach 42

Figure 3.3. Billingsgate study site 43

Figure 3.4. Site 2 Trader's Car Park, Billingsgate Market 44

Figure 3.5. The four study species 46

Figure 3.6. Field experiment enclosure 52

Chapter 4:

Figure 4.1. Relationship between abundance and size of prey items in the environment at Billingsgate. 55

Figure 4.2. Population density plotted against standardized $\log_n$ kleptoparasitism rate 58

Figure 4.3. Prey size plotted against standardized $\log_n$ kleptoparasitism rate 58

Chapter 5:

Figure 5.1. Bar chart showing a comparison of the rate at which each species age-class committed and was the host to kleptoparasitism at Billingsgate 75

Figure 5.2. Bar chart showing a comparison of the rate at which each species age-class committed and was the host to kleptoparasitism at Brancaster 84

Chapter 6:

Figure 6.1. Aerial photograph of the Billingsgate study area (Trader's Car Park) 112

Figure 6.2. Frequency and distribution of foraging patches occurring at Billingsgate 113

Figure 6.3. Location of the foraging patch hotspot in the Trader's Car Park at Billingsgate 114

Figure 6.4. The five loafing areas at Billingsgate 115

Figure 6.5. Aerial photograph of the study area highlighting in red each of the ground level measurement points from the patch hotspot in the Trader's Car Park to the loafing area boundary points on buildings 1-5 116

Figure 6.6. Image of the enclosure pen used for provisioning studies 117

Figure 6.7. Bar chart showing distribution of dominant and subordinate birds as the distance of loafing buildings from the patch hotspot increased 120

Chapter 7:

Figure 7.1. Flow diagram showing the dynamics of the Billingsgate foraging population for the single-species model 133

Figure 7.2. Searching pathway for an AGG forager 140

Figure 7.3. Searching pathway for an ST forager 140

Figure 7.4. Phase diagram showing the decision points for an AGG searcher that has just encountered a handler 141

Figure 7.5. Phase diagram showing the decision points for a ST searcher that has just encountered a handler 142

Figure 7.6. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked AGG 145

Figure 7.7. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked AGG 146

Figure 7.8. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked ST 147

Figure 7.9. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked ST 148

Figure 7.10. Phase diagram showing the decision points for handler that is challenged AGG in a population that surrenders food items 149

Figure 7.11. Phase diagram showing the decision points for handler that is challenged ST in a population that surrenders food items 150

Figure 7.12. Phase diagram showing the decision points for a handler that is attacked AGG by a mutant searcher in a population which does not use kleptoparasitism 151

Figure 7.13. Phase diagram showing the decision points for a handler that is attacked ST by a mutant searcher in a population which does not use kleptoparasitism 152

Figure 7.14. Graph showing regions of the foraging parameter space at Billingsgate where each of the 5 possible ESS's occurs for different population density values (P) and food discovery rates ($v_f f$) 157

Figure 7.15. Foraging strategies used in the region of parameter space in which they are ESS's 163

Figure 7.16. Foraging strategies used in the region of parameter space in which they are not an ESS 164

Tables

Chapter 1:

Table 1.1. Taxonomic bird families containing large numbers of kleptoparasites 23

Chapter 2:

Table 2.1. Summary of general research aims and key questions 26

Table 2.2. Ecological conditions facilitating kleptoparasitism 27

Table 2.3. Payoffs for the asymmetric Hawk-Dove-Bourgeois-X game when the value of the food item differs between the owner (V) and the challenger for a food item (v) 33

Chapter 3:

Table 3.1. Behaviours constituting strategies of aggressive, stealth, and scramble kleptoparasitism 48

Table 3.2. Data used to obtain a standardised bill length measurement in millimetres 49

Chapter 4:

Table 4.1. Summary of generalised linear models 57

Table 4.2. Differences in prey size (Billingsgate: N = 593; Brancaster: N = 86) and population density (Billingsgate: N = 183; Brancaster: N = 86) between the two study sites. 59

Chapter 5:

Table 5.1. Species composition of populations at Brancaster and Billingsgate calculated using headcounts at patches, and total population headcounts 66

Table 5.2. Billingsgate population composition by species and age 69

Table 5.3. Kleptoparasitic interactions at Billingsgate 70

Table 5.4. Summary of kleptoparasitic behaviours committed by Billingsgate gulls differentiated by species, age, type, and level of success experienced by kleptoparasites 71

Table 5.5. Summary of Billingsgate host data showing hosts (victims) of kleptoparasitic attempts by species, age, type and percentage of time they were successfully parasitized 72

Table 5.6. Frequency with which hosts defended and surrendered food items against kleptoparasitic attacks 72

Table 5.7. Strength of association between species at Billingsgate and kleptoparasitism rate between those species 73

Table 5.8. Strength of association between age-classes at Billingsgate and kleptoparasitism rate between those age-classes 73

Table 5.9. Weighted kleptoparasitism and host scores for each species age-class at Billingsgate 74

Table 5.10. Contingency table showing the frequency scores for success and failure in their use of kleptoparasitic strategies for status categories at Billingsgate 76

Table 5.11. Contingency table showing the frequency scores with which aggressive and stealth kleptoparasitic strategies were used by dominant and subordinate gulls at Billingsgate 76

Table 5.12. Brancaster population composition by species and age 77

Table 5.13. Kleptoparasitic interactions at Brancaster 78

Table 5.14. Summary of kleptoparasitic behaviours committed by Brancaster gulls differentiated by species, age, type, and level of success experienced by kleptoparasites 79

Table 5.15. Summary of Brancaster host data showing hosts (victims) of kleptoparasitic attempts by species, age, type and percentage of time they were successfully parasitized 80

Table 5.16. Frequency with which hosts defended and surrendered food items against kleptoparasitic attacks 80

Table 5.17. Strength of association between species at Brancaster and rate of kleptoparasitism between those species 81

Table 5.18. Strength of association between age-classes at Brancaster and kleptoparasitism rate between those age-classes 82

Table 5.19. Weighted kleptoparasitism and host scores for each species age-class at Brancaster 83

Table 5.20. Contingency table showing the frequency scores for success and failure in their use of kleptoparasitic strategies for status categories at Brancaster 85

Table 5.21. Contingency table showing the frequency scores with which aggressive and stealth kleptoparasitic strategies were used by dominant and subordinate gulls at Billingsgate 85

Table 5.22. Frequency of kleptoparasitism committed by each age-class and hosted by each age-class at Billingsgate 95

Table 5. 23. Mixed-strategies for conspecific kleptoparasitism at Billingsgate 107

Chapter 6:

Table 6.1. Mean flight distances in metres from each of the 5 loafing buildings to the hotspot for foraging patches 116

Table 6.2. Contingency table showing the frequencies with which different status groups occurred in the two locations at Billingsgate 119

Table 6.3. Contingency table showing the frequencies with which different status groups loafed on the main buildings (1-5) 120

Chapter 7:

Table 7.1. Model notation 132

Table 7.2. Conditions under which it is advantageous to challenge and resist/ defend in the Billingsgate population 153

Table 7.3. Conditions that need to be satisfied for each of the twelve candidate foraging strategies to be an ESS 155

Table 7.4. Parameter values used to investigate the regions of parameter space occupied by different ESS's at Billingsgate 156

Table 7.5. Mean values for model parameters obtained from Billingsgate foraging data 159

Table 7.6. Equilibrium density results for the Billingsgate population at parameter values of $(t_h = 0.42, t_c = 0.14, t_a = 0.26)$ 161

Table 7.7. Descriptive statistics showing duration of focal animal observations on foragers at Billingsgate 162

Table 7.8. Frequency with which strategies at Billingsgate were used in the region of parameter space where they were an ESS and regions where they were not an ESS 165

Abstract

This thesis investigated kleptoparasitism in mixed-species foraging aggregations of gulls (*Laridae*). Kleptoparasitism, or food stealing, is a strategy used frequently by gulls. Gull populations are increasing in urban areas despite declining overall. Understanding the role of kleptoparasitism in aiding gulls to invade urban environments was a central aim of this research. A second aim was to develop a model of kleptoparasitism using a compartmental modelling approach from evolutionary game theory and to test this using real foraging data.

Fieldwork was undertaken at two study sites: a coastal site (Brancaster beach, Norfolk, UK) and an urban site (Billingsgate Market, London, UK). The focal species were the Great black-backed gull (*Larus marinus*), Herring gull (*Larus argentatus*), Black-headed gull (*Chroicocephalus ridibundus*), and Common gull (*Larus canus*), these species forage together but differ in size and competitive ability. Foraging at the sites was recorded and analysed for kleptoparasitic incidents. Three kleptoparasitic strategies were considered: *aggressive*, *stealth* and *scramble kleptoparasitism*.

Four studies were conducted: Study 1 investigated differences in the rate of kleptoparasitism between the study sites and assessed the ecological predictors of this difference. The results showed kleptoparasitism was higher at the urban site and higher population density was the best predictor of this. Kleptoparasitism may aid invasion and increase the range of environments a gull can tolerate by helping them meet their energy needs in novel environments.

Study 2 described the patterns of kleptoparasitic behaviour observed at both sites. Large species used aggressive kleptoparasitism against smaller species, and smaller species used stealth kleptoparasitism when stealing from larger species. The use of stealth kleptoparasitism by smaller, subordinate foragers was identified as an empirical example of a Marauder strategy. Kleptoparasitic strategies were used flexibly to compete for resources against opponents of different competitive abilities.

Study 3 examined what strategies, other than kleptoparasitism, subordinate foragers at Billingsgate used to compete for resources. Subordinate gulls foraged for longer, stayed closer to potential food locations, arrived first at patches and took more risks to obtain food than dominants.

Study 4 developed a game-theoretical model and compared this model against the foraging data for Billingsgate. The results indicated the density of different foraging behaviours at Billingsgate may be at an equilibrium, but only 23% of foragers were using evolutionarily stable strategies. This result was attributed to a one-species model being used to describe a population containing three species of differing competitive ability. Further work applying game-theoretical models to field data is needed to assess how effectively gulls use kleptoparasitic strategies, particularly in novel environments such as urban areas.

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Preface

0.1 – Introduction

In this thesis I report research conducted in behavioural ecology. That research focuses on the adaptive value or current utility of kleptoparasitic foraging behaviours in gull (*Laridae*) populations faced by different environmental parameters.

Kleptoparasitism has in the past been the focus of extensive research (Verbeek, 1977a; Verbeek, 1977b; Brockmann & Barnard, 1979; Barnard & Thompson, 1985; Barnard & Sibly, 1981; Barnard, 1984), however, interest in kleptoparasitism seems to have waned among empirical researchers in recent times and the baton for conducting research into this fascinating behaviour has been carried by theoretical researchers through the development of mathematical models in disciplines such as evolutionary game theory (Broom & Ruxton, 1998; Broom & Ruxton, 2003; Broom, Luther & Ruxton, 2004; Broom & Rychtar, 2007; Broom & Rychtar, 2009; Hadjichrysanthou & Broom, 2012). These theoretical kleptoparasitism models have provided valuable insights into the types of behaviours we should expect to be successful when individuals in groups compete for resources. However, little work has been done to compare or test the findings of kleptoparasitism models against the behaviour of real foraging populations or to use these approaches to model a population of foraging animals. A primary reason for this is the difficulty in finding populations of real foragers that match all the simplifying assumptions necessary to fully specify a mathematical model.

In this research I sought to address this disconnect between theoretical and empirical research by identifying a suitable study population, developing a game-theoretical model of that study population and comparing the model results against real foraging behaviour. To do so I adopted the compartmental modelling approach pioneered by Broom and colleagues (Broom & Ruxton, 1998; Broom & Ruxton, 2003; Broom, Luther & Ruxton, 2004) and modelled a population of gulls that aggregate to forage in an urban area.

It is hoped that the studies in this thesis will resurrect some interest in kleptoparasitism research amongst behavioural ecologists and other empirical researchers. There are still many interesting questions to be answered about kleptoparasitism. The gull populations that were the focus of this research are invasive species that are found across a range of environments. The increasing urbanisation of the planet as human populations continue to grow has led to a growing interest in research into invasive species and the behaviours that allow them to colonise and tolerate rapidly changing conditions. I would suggest that, for the gulls that were the focus of this research, kleptoparasitism is one of the most important of these behaviours and is worthy of further investigation.

0.2 – Outline of the thesis

This thesis is developed over four stages. Part 1 contextualises the research and introduces the literature that is most relevant to the studies that were conducted. This is achieved through two chapters. Chapter 1 introduces *Social Foraging Theory* and situates the thesis within this area of research, before moving on to discuss models of kleptoparasitism and why gull populations were chosen as a model system for the kleptoparasitism research conducted. Chapter 2 reviews the literature on kleptoparasitism that was of most relevance to the studies being conducted, outlines four general research aims of the thesis and introduces the key questions used to address those research aims.

Part 2 outlines the data collected and the field studies conducted. This is covered by chapters 3, 4, 5 and 6. Chapter 3 is a methods chapter that describes the field sites, study species and the fieldwork conducted to collect the data used for all four studies. Chapter 4 covers study 1 which sought to assess if there was a difference in the rate of kleptoparasitism between the two field sites used and to investigate which aspects of the ecology of these two sites best predicted any difference that was seen. Following on from this, having described the global difference in the rate of kleptoparasitism between the two sites in study 1, Chapter 5 contains the analyses conducted for study 2 which looked at the data within each study site and described the main patterns of kleptoparasitism that were observed. This chapter covers a lot of material and analyses in depth which species and age-classes attempted kleptoparasitism against each other, and what strategies they used to do this. One analysis conducted in this chapter examines the kleptoparasitism strategies used by subordinate foragers to try and steal from larger, more dominant individuals. Chapter 6 outlines study 3 which looked further at the behaviours of subordinate foragers. This chapter focuses solely on the urban study population at Billingsgate Market by investigating the ways in which subordinate individuals compete for resources other than through the use of kleptoparasitic strategies.

Part 3 contains the modelling work conducted. This is described in Chapter 7, which outlines the development of a game-theoretical model of a population of the same size and able to use the same kleptoparasitic strategies as the Billingsgate study population. The real foraging data collected from Billingsgate was then inputted into the model to test to see if the density of different foraging behaviours in the Billingsgate population was at an equilibrium and to analyse whether individual foragers were making good behavioural decisions by using evolutionarily stable strategies in the correct environmental conditions.

Part 4 concludes the thesis. Chapter 8 is a chapter containing concluding remarks which summarises the research conducted and the main findings from each of the four studies. A critical appraisal is also undertaken of the fieldwork methods, research questions addressed and results of the studies. The limitations of the research are acknowledged and recommendations for further work are highlighted.

(1)

Chapter 1 – Social foraging theory, models of kleptoparasitism and gulls (*Laridae*) as a model system for studying kleptoparasitism

1.1 – Introduction

Kleptoparasitism is the theft of already procured food by one individual from another and it occurs when animals search for food in groups. It is one of the most widespread forms of exploitation found in nature. In this chapter I will outline the relevant theoretical perspectives in the study of kleptoparasitism, discuss the use of gulls (*Laridae*) to study kleptoparasitic behaviour and explain why an urban population of gulls was the focus of the research conducted for this thesis.

1.2 – Social Foraging Theory

Foraging refers to all the ways in which animals search for, identify, pursue, capture, process and consume their various food sources, including competitive and cooperative interactions with other foragers. Foraging behaviour can be a solitary activity or a collective action, such as the cooperative hunting seen in lion prides. However, a large amount of foraging consists of competitive interactions between individuals that aggregate where limited food sources are located. Foraging research within behavioural ecology falls under the umbrella term of *foraging theory* (Stephens & Krebs, 1986).

There are two facets to foraging research. First, mathematical models of foraging are constructed to demonstrate the evolutionary logic underlying behaviour and to assess what behaviours we should expect to see evolve (Ydenberg, Brown & Stephens, 2007). Second, such models are analysed and refined using real foraging behaviour and tested through observational or experimental methods in the laboratory or field. These two facets of foraging theory are meant to be synergistic partners (Ydenberg et al. 2007).

Foraging theory can be separated into two main domains of interest, *conventional foraging theory* which focuses on individual foraging behaviour (Giraldeau & Caraco, 2000; Stephens & Krebs, 1986); and *social foraging theory* (Giraldeau & Caraco, 2000), which is concerned with the adaptive value of individual decisions when foraging in a group. This thesis focuses on a particular foraging behaviour (kleptoparasitism) that occurs when animals search for food in groups, situating this research within the domain of social foraging theory.

The benefits of social foraging may include an increase in individual feeding rate, and a reduction in the amount of variance an individual is likely to experience in the rate at which it encounters prey (Ranta, Peuhkuri, Laurila, Rita, & Metcalfe, 1996). These benefits result from the

presence and behaviour of others acting as a cue to the location and availability of food sources, and from groups being more effective at finding food than a solitary individual. For a number of species, a further benefit to group foraging is a reduction in predation risk, both through the dilution of risk with increasing group size and increased vigilance from the multiple pairs of eyes in a group providing early warning of potential dangers.

Foraging in a group can also have considerable costs for the individual. Resource competition will increase with group size. A higher density of consumers will not only result in resources being depleted more quickly but can also lead to an individual feeding less efficiently due to interference effects caused by the presence of others simultaneously exploiting a patch (Sutherland, 1983). Additionally, competition for resources when foraging socially can result in increased aggression and kleptoparasitism, which have a significant impact on foraging behaviours in a group (Giraldeau & Caraco, 2000).

The basic principle of social foraging theory is that the best tactic for a forager to use depends on what other foragers in the population are doing (Waite & Field, 2007). Giraldeau and Caraco (2000) defined this as the "concurrent economic interdependence among different individuals' payoffs and penalties" (p.3). This essentially means that the consequences of an individual's foraging decisions depend on the actions of that individual, as well as the behaviours of others. To qualify as social foraging the interaction under consideration must involve at least two individuals influencing each other's energetic costs and benefits (Giraldeau & Caraco, 2000). A critical implication of this economic interdependence is that social foraging models require game-theoretic solutions.

Game theory is the analysis of the strategic decisions made when two or more individuals compete over some resource. The intention is to identify the optimal decision rational players should make to maximise their chance of victory. Game theory has wide applicability when examining competitive interactions, and *Evolutionary game theory* is the biological branch of game theory. The payoffs in an evolutionary game are represented as losses or gains in fitness and natural selection is viewed as the rational agent that has selected for effective behavioural strategies.

Game theory uses the concept of stability to investigate what to do when the best decision to make depends on what other individuals are doing (Ydenberg, 2010). There are several game theoretic solution concepts based around stability, two that are of value to behavioural ecologists are the *Nash equilibrium* (Nash, 1951) and *Evolutionarily Stable Strategy (ESS)* (Maynard Smith & Price, 1973). These two solution concepts are closely related. A Nash equilibrium can be defined as a set of strategies among the players of a game, which when each player plays their Nash strategy no individual can improve their payoff by changing their decision (Ydenberg et al. 2007). Nash equilibrium strategies are most frequently used when analysing interactions between humans using game theory (Broom & Rychtar, 2013).

An ESS is a set of strategy choices which when common in a population cannot be beaten or invaded by an alternative strategy (Davies, Krebs & West, 2012). We should not necessarily expect to see just one strategy that is the 'best' being played by all members of a population. When multiple

strategies exist then the evolutionary stable solution is the frequency at which, however many strategies are being used, each individual is receiving their best payoff in the given interaction, so there is no incentive for any individual to change the strategy it is using. An ESS therefore possesses the properties of both stability and optimality (Giraldeau & Caraco, 2000).

Social foraging models are concerned with the adaptive significance of individual behaviour when individuals in groups compete for resources and these models use the concepts of the Nash equilibrium (Nash, 1951) and ESS (Maynard Smith & Price, 1973) from game theory as solutions. Appendix A describes a classic model from evolutionary game theory analysing what happens when individuals in a population of animals compete over a resource and Appendix B provides formal definitions of Nash equilibrium and ESS.

According to Giraldeau & Caraco (2000) social foraging theory addresses two core questions these are: 1) Questions of *group membership*, whether to leave or join a group in a given set of ecological conditions. 2) *How to exploit resources* within foraging groups. The first of these questions addresses how foragers should distribute themselves in relation to resources given the competitors they face, the second assumes group membership as a constraint of the population and instead assesses how an individual should behave to best exploit resources when in those groups. It is this second question that is the central concern of this thesis.

Research addressing the second question, how resources should be exploited, has focused on a key decision involving two behaviours that are amongst the most widely studied in behavioural ecology. This is the decision whether an individual should search for its own food, or join the finds of food discovered by other individuals. A number of terms are used in the literature to describe these behaviours, amongst the most common are *finding and joining*, or *producing and scrounging*.

The issues of interest in such research are the conditions that promote the theft of food among social foragers, the behavioural strategies used to carry out this theft, and the evolutionarily stable level of food theft. The term frequently used to describe these food stealing behaviours is kleptoparasitism. As described in the introduction to this chapter, kleptoparasitism is the theft of already procured food (Brockmann & Barnard, 1979) and it is widespread in nature, having been observed in a number of species across taxonomic groups. The significance of kleptoparasitic behaviour is that it is a way of avoiding foraging costs by exploiting food discovered by another individual's effort (Giraldeau & Caraco, 2000).

Giraldeau & Caraco (2000) have also highlighted that kleptoparasitism is not a unitary concept. These authors suggest that there are three main types of kleptoparasitism: *Aggressive kleptoparasitism*, usually where one individual aggressively acquires and dominates the resource. *Scramble kleptoparasitism*, where resources are exploited simultaneously by several competitors with little aggression; and *stealth kleptoparasitism*, where individuals steal food while avoiding direct interactions with the producer or owner of the food item (Giraldeau & Caraco, 2000).

1.3 – Models of kleptoparasitic behaviour

Several approaches have been taken to modelling kleptoparasitism. Three approaches that have made significant contributions to the social foraging literature on kleptoparasitic behaviour are *Information Sharing Models*, *Producer-Scrounger Models*, and the *kleptoparasitism models* developed by Broom and colleagues (Broom & Ruxton, 1998; Broom, Luther & Ruxton, 2004).

1.3.2 – Information Sharing Models: The simplest models addressing kleptoparasitic interactions are called *Information Sharing (IS)* models. At their most basic IS models assume that each forager in a group searches for its own food and seeks opportunities to scrounge at the same time (Giraldeau & Beauchamp, 1999). The assumption is made that performing these behaviours concurrently is possible and no opportunity to find food is lost by looking for opportunities to steal.

A number of other assumptions are evident in basic IS models, such as assumptions about the divisibility of food, and the equality of competitive abilities between members of the foraging group. Under such parameters, where there is no cost to scrounging, the only stable strategy is for all group members to search for food, but also to join at every opportunity (Giraldeau & Beauchamp, 1999). However, few foraging situations in nature are likely to meet the simplifying constraints of basic IS models.

1.3.3 – Producer-Scrounger Models: Game-theoretic *Producer-Scrounger (P-S)* models seek to produce a more realistic alternative to IS models when analysing kleptoparasitic interactions. Unlike IS models, P-S models treat the options of searching for food (Producer) and joining (Scrounger) as discrete and incompatible alternatives (Barnard & Sibly, 1981). So, at any one time individuals in the foraging group are either producing or scrounging, they cannot do both concurrently. There are good reasons to suggest that this can be a realistic assumption as an animal looking in one place for food cannot simultaneously be looking somewhere else for scrounging opportunities.

The relevance of this incompatibility is that it introduces the concept of *frequency-dependence* into the evolutionarily stable solution. This means that the benefits obtained by an individual when using either strategy are affected by how rare or common that strategy is in the foraging group. This is because an animal that is using the scrounger tactic is not contributing to the quantity of food being discovered by the group. The more individuals that scrounge, the fewer individuals there are producing food for them to parasitize, so the payoff for all individuals in the group decreases. This can lead to fluctuations in the prevalence of the two strategies as their fitness changes with how common they are (Alcock, 2005). The concept of frequency-dependent selection is discussed in more detail in Appendix C.

The most basic P-S models treat membership of the foraging group or population of interest as fixed. So, a forager cannot leave the group and is therefore stuck in the foraging environment in which it finds itself. This is a constraint assumption built-in to make analysis of the model more manageable (Giraldeau & Caraco, 2000). However, in some natural situations it is plausible that the ability of foragers to leave a group and search elsewhere may be constrained by a lack of other food sources making this a worthwhile assumption in some cases.

An additional constraint built into many P-S models is known as the *finder's advantage* (Giraldeau & Caraco, 2000). This is the assumption that the finder of a food item will be able to consume some quantity of its discovery before scroungers arrive to exploit it. The larger the quantity the finder (producer) can consume the lower the benefit gained from using the scrounger tactic.

Empirically demonstrating the frequency-dependent payoffs and ESS for P-S models has proved difficult as the most effective and clear demonstrations require identifying a study species, or model system, in which individuals specialise in one or the other strategy. However, in many cases individuals may randomise between the two strategies and use a mixed strategy (Appendix B) (Giraldeau & Caraco, 2000). The ratio of an individual's mix of the two strategies will still represent a valid demonstration of a negative frequency-dependent ESS (Appendix C), but the difficulty lies in identifying clearly when individuals are using each strategy and calculating their payoffs over a period of observed foraging (Giraldeau & Caraco, 2000); without accurately identifying the boundaries of an animal's bout of foraging the observed ratio of producer to scrounger may lead to a biased assessment of the rate at which each strategy is used.

1.3.4 – Kleptoparasitism models: As stated previously there are three issues of interest in research on kleptoparasitism, these are: the conditions that promote the theft of food among social foragers, the behavioural strategies used to carry out this theft, and the evolutionarily stable level of food theft. The IS and P-S models deal with the evolutionarily stable level of theft in a population by analysing the equilibrium frequency of producers to scroungers. Key features of these models are that food items are highly divisible, can be split between producers and scroungers and that the costs incurred by foragers are energetic costs. However, IS and P-S models provide little insight into the environmental conditions that promote kleptoparasitism or into understanding how the ability to use different strategies of kleptoparasitism will influence behaviour. An alternative approach to modelling kleptoparasitism that considers the equilibrium frequency of producers to scroungers as well as assessing what is the best behavioural decision for an individual forager to make in different environmental conditions has been developed from a kleptoparasitism model by Broom and Ruxton (1998).

Broom and colleagues, over a number of years, have developed a series of game-theoretical models (Broom & Ruxton, 1998; Broom & Ruxton, 2003; Broom, Luther & Ruxton, 2004; Broom & Rychtar, 2007; Broom & Rychtar, 2009; Hadjichrysanthou & Broom, 2012) that have systematically explored the kleptoparasitic foraging space, often changing key variables of the model one at a time to examine how this influences behaviour. For example, the initial model in this series by Broom & Ruxton (1998), based on a mechanistic model by Ruxton and Moody (1997), considered a population of foragers where a searcher, upon encountering another forager handling a food item, was faced with the decision whether to ignore that handler and keep searching for food items or attempt to steal food from the handler. The handler was assumed always to defend its food item from attempts to steal it. In a later model (Broom, Luther & Ruxton, 2004) the assumption that the handler always defends was relaxed and the handler was given the option of whether to defend the food item or surrender it without a fight. Changing the complexity of the behavioural decisions involved in small

increments like this has numerous potential consequences which, when combined with different parameter values such as the amount of food available in the environment and the length of time it takes to win a fight, will influence the optimal and stable strategies that will be seen in a foraging population.

The key features of the models developed by Broom and colleagues are a foraging population of a fixed density, a compartmental approach to modelling the population where individuals can be in only one behavioural state at a time (for example, handling or searching or fighting) and the rates of change between the behavioural states are described by a system of differential equations, the assumption that food items come in single units that have limited divisibility and are consumed completely by an individual forager, as well as the use of time to model all foraging costs. For example, searching for food items has a cost to the forager in terms of time, handling a food item has a time cost, and engaging in a fight to either try to steal or keep hold of a food item has a cost in terms of time. The costs incurred by the forager for making the incorrect behavioural decision accumulate over time because, whilst it is engaged in the wrong behaviour, it loses the opportunity to be doing something else that could more quickly lead to the acquisition of a food item and is thereby more profitable.

The series of models developed by Broom and colleagues can be extended incrementally in many ways to consider various constraints and assumptions in relation to the environment and foragers. For example, the complexity of a basic model can be increased by introducing competitive differences between foragers in the population and increasing the number of behavioural strategies they can use. These models, whilst more complex to find solutions for, still assume a forager seeks to maximise its rate of food or energy intake whilst foraging and this is achieved by choosing the behaviours that minimise the amount of time needed to obtain and consume food items. An animal that maximises its rate of food intake will, on average, have higher survivorship than other foragers with whom it is competing and this higher feeding rate is assumed to translate into a fitness advantage for that individual and the genes that encode for the successful strategy it uses.

The kleptoparasitism models developed by Broom and colleagues have provided many theoretical insights into the behaviours we should expect to be prevalent in a population, however, little empirical work has been conducted to test these models or to compare the predictions of this kleptoparasitic modelling approach against the behaviour of real foragers. This may be because it is difficult to find real foraging populations that match all the simplifying assumptions necessary for comparison against a mathematical model. If suitable study populations can be identified the kleptoparasitism models developed by Broom and colleagues represent a valuable means of investigating kleptoparasitic foraging behaviour. The kleptoparasitism models of Broom and colleagues were a key method used to investigate kleptoparasitic behaviours in this thesis and, as discussed in the next section, foraging aggregations of gulls were the study populations used as a model system for this research.

1.4 – Kleptoparasitism and gulls

Certain taxonomic classes contain large numbers of kleptoparasites, so research has focused more on some species than others. For example, among the arthropods a great deal of research has examined the kleptoparasitic behaviours of certain species of arachnid (Vollrath, 1984). However, the class of animals that have received the most intense research focus are the birds.

Many bird species engage in kleptoparasitism, both inter and intra-specifically, with differing levels of investment. Some bird species specialise in an almost entirely parasitic lifestyle, such as the skuas (*Stercirariidae*) and frigatebirds (*Fregatidae*). In other species kleptoparasitism is just one of a number of foraging strategies used. Brockmann and Barnard (1979) conducted a review of kleptoparasitic incidents reported in the ornithological literature over a forty-year period. From this they identified the taxonomic groups containing the largest number of kleptoparasitic species.

The families of birds with the highest numbers of kleptoparasites, identified by Brockmann and Barnard (1979), were the *Falconidae* (falcons, kestrels, caracaras), *Accipitridae* (hawks, eagles, harriers, old world vultures), and the *Laridae* (gulls). As can be seen from Table 1.1, the presence of kleptoparasitism in the *Laridae* is much more pronounced than the other families with 23 of the 88 species of gull making use of kleptoparasitic strategies.

Gull species are found across a variety of habitats around the world (Pons, Hassanin & Crochet, 2005), and have been noted for their tendency to colonise novel environments (Rock, 2005). Additionally, as members of the sub-order *Charadrii* they are one of only two groups of modern birds known to have been around since the Cretaceous period over 65 million years ago (Proctor & Lynch, 1993). The significant investment of gull species in kleptoparasitism highlights the importance of this strategy to those species, and suggests kleptoparasitic behaviours have played an important role in aiding the radiation and longevity of this family, making them an important group of birds for research into kleptoparasitism.

Gull species reach reproductive maturity between their third and fourth year, are iteroparous, and can live up to 30 years. The breadth of their diet and diversity of foraging behaviours has led to them being described as generalist, or opportunist, species. This lack of specialisation has been suggested as the basis for the gull's adaptability (Tinbergen, 1953), and presence in many different environments.

Gulls can be highly gregarious, but their sociality is not complex in the same way as other species, such as the fission-fusion societies of primates or the reproductive territories with helpers seen amongst the *Corvidae*, and there is no evidence to suggest that gulls remain in family bonded kin-groups outside the breeding season or maintain links to offspring once they have fledged. Much of the sociality of gulls outside the breeding season consists of mixed-species feeding aggregations around ephemeral food sources. These aggregations are complex competitive situations of the type likely to encourage kleptoparasitism as a foraging strategy.

Table 1.1. Taxonomic bird families containing large numbers of kleptoparasites. Adapted from Brockmann and Barnard (1979).

Taxonomic Family	No. of species in family	No. of kleptoparasitic species in family	% of species using kleptoparasitism
Faconidae	298	31	10.4
Accipittridae	226	22	9.7
Laridae	88	23	26

According to several conservation agencies certain species of *Laridae* have shown significant population declines in the UK over the past fifty years. This is true of the Great black-backed gull (GBB: *Larus marinus*) which experienced an 11% decline in the non-breeding population in the 20 years up to 2004 (Reid, 2004). This species is now amber-listed in the most recent update of the birds of conservation concern census (Eaton et al. 2015) making them a species whose conservation status is becoming an increasing priority. More critically, Herring gull (HG: *Larus argentatus*) populations in the UK have experienced a significant long-term breeding decline of 48% between 1969 and 1988, and a further 13% decline between 1988 and 2004 (Madden & Newton, 2004). These trends have resulted in the Herring gull being put on the red-list, making them a conservation priority in the UK (Eaton et al. 2015). Amongst smaller gull species, the Black-headed gull (BHG: *Chroicocephalus ridibundus*) and Common gull (CG: *Larus canus*) are two of the most recognisable UK gull species, these species have also been amber-listed in the birds of conservation concern census (Eaton et al. 2015).

Despite these downward trends, it has also been noted that gull populations for some species are increasing in urban areas (Rock, 2005), this is true of both the GBB and HG. This juxtaposition of population trends in the two environments would suggest that the ecology of gull species may be changing, perhaps due to changes in their traditional food sources, such as declines in fishing stocks, and perhaps also due to opportunities afforded to them to exploit the sites and waste created by humans in urban areas. These factors need not be mutually exclusive and may, in combination with other drivers, provide an explanation as to why gull populations are increasing in urban environments whilst declining elsewhere. A comprehensive understanding of this situation will, however, require an investigation of the behavioural strategies of gulls that are playing a part in this shift to urban spaces.

Laridae are clearly a good model system for research into kleptoparasitism. The shift in gull populations to urban environments is an area requiring further research to understand the behaviours that helped make this change to novel environments possible. For these reasons gull species' of the family *Laridae* were the focal species' used in this research and the main study population was a mixed-species population of gulls that forage for food at an urban site.

1.5 – Summary

In this chapter I have outlined some of the principles of social foraging theory as a major research area in behavioural ecology. Social foraging theory addresses questions about how to behave when exploiting food in groups. The notion of economic interdependence was discussed and I outlined the need for game theoretic solutions to social foraging interactions, as the best decision a forager can make depends on what other group members are doing.

A key behavioural decision analysed in social foraging research is under what circumstances a forager should steal food from other group members as opposed to searching for its own food. This behaviour is called kleptoparasitism and I outlined three models of kleptoparasitic behaviour. The compartmental approach to modelling kleptoparasitism developed by Broom and colleagues was outlined as a key method used in this thesis to investigate kleptoparasitic foraging behaviours. This modelling approach allows the inclusion of many realistic assumptions about animal populations but has not yet been compared against data from real foraging populations.

This thesis conducted research into kleptoparasitism using mixed-species foraging aggregations of gulls (*Laridae*), giving particular focus to a population of gulls in an urban environment. In this chapter I have justified why gulls were used as the model system in this research and explained why a population in an urban environment was the focus of research. Gulls invest heavily in kleptoparasitic behaviours and have recently shown a significant shift in ecology, with populations declining in traditional areas but simultaneously increasing in urban environments. This presented an opportunity for investigating the function of kleptoparasitism for gulls across environments whilst giving particular attention to the importance of this behavioural strategy in allowing gulls in urban environments to meet their energy demands. In the next chapter I outline the main research aims addressed in this thesis and discuss the relevant literature that justified those research aims.

(2)

Chapter 2 – Research aims

2.1 – Introduction

In the previous chapter I outlined some of the background concepts relevant to this thesis and discussed the use of gulls as a model system for studying kleptoparasitism. In this chapter I will outline the main research aims addressed in this thesis and discuss the existing literature of most relevance to these aims.

2.2 – Study populations and summary of the research aims

Two study populations were used in this research. The first a foraging population of gulls in a coastal environment, assumed to be typical of the shoreline foraging ecologies encountered by gulls throughout much of their evolutionary history. The second a foraging population in an urban environment. The coastal site was Brancaster Bay, Norfolk, UK, and the urban site was Billingsgate Market, London, UK. The study population at Brancaster forage on the foreshore at low tide and the Billingsgate population in the urban environment forage for food waste in the car park areas of a seafood market (See Chapter 3 for a detailed description of these two sites).

Four general research aims were addressed through four studies using these study populations. Table 2.1 provides a summary of the four research aims, the questions making up those aims and the four studies used to answer those questions. In the following sections I provide a detailed discussion of each of the four research aims.

Table 2.1. Summary of general research aims, key questions and studies used to achieve those aims.

Research Aim	Key Questions	Study
To assess the role of kleptoparasitism in helping gull species invade novel environments	1. Does kleptoparasitism use differ across environments?	1
	2. How do ecological variables influence kleptoparasitism?	1
To investigate kleptoparasitic foraging behaviour in competitively asymmetric populations	3. How do differences in competitive ability influence kleptoparasitic behaviours?	2
	4. How does ability to use different types of kleptoparasitism influence the behaviour of kleptoparasites and the responses of hosts?	2
	5. Is Stealth kleptoparasitism an example of a Marauder Strategy (Strategy X)?	2
An examination of the foraging behaviours used by subordinate individuals in mixed-species social groups	6. Beyond kleptoparasitism what other behavioural strategies do subordinate foragers use to compete for resources?	3
To develop a P-S model of a wild bird population	7. Is the density of producers to scroungers in the population at an equilibrium?	4
	8. Does kleptoparasitic behaviour match the ESS predictions for the environmental conditions encountered?	4

2.3 – Research Aim 1: To assess the role of kleptoparasitism in helping gull species invade novel environments

Increasing urbanization has undoubtedly impacted upon biodiversity. Much research has been developed in this area and much has concentrated upon the characteristics shared by invasive species, such as dietary generalism and diversity of foraging behaviours (Reader & Laland, 2003).

Invasion into novel environments, such as urban spaces, requires finding solutions to a number of problems, arguably the most pressing of which is acquiring food. Brockmann and Barnard (1979) outlined several ecological conditions that appear to facilitate the use of kleptoparasitism as a strategy (Table 2.2). The Brockmann and Barnard (1979) paper contains an implicit acknowledgement that, in some species, kleptoparasitism is a foraging strategy that is flexibly used as environmental parameters change. These changes could be within the same environment over time, or, in particularly mobile species such as birds, the same ideas could equally apply to how behaviour changes as the organism moves from one environment to another. As a behavioural strategy that appears to be employed flexibly as environmental conditions change, one might expect that kleptoparasitism could play a significant role in, not only, allowing the organism to survive across

a range of habitats, but also in allowing the organism to converge on an adaptive response to the newly encountered conditions.

Table 2.2. Ecological conditions facilitating kleptoparasitism. Adapted from Brockmann and Barnard (1979).

Ecological Condition	Description
Large concentrations of hosts	Necessary for klepto to become more than an occasional strategy. Eg. Large seabird colonies and large aggregations of wader species.
Large quantities of food	Provide significant opportunities for theft and the systematic use of klepto. Eg. Colony nesting species provide a central place where the host must return with food.
Large, high quality, food items	Large items tend to be more calorific and worth stealing. Eg. Gulls target terns with larger items. Plant material is rarely the object of klepto interactions.
Food supply predictable	Klepto is more common when the host's behaviour is predictable. Eg. Hosts returning to the same nest site with food.
Food visible	Provides the parasite with cues as to the presence of food. Eg. Large fish held in bill or talons.
Food shortage	Klepto is more common when conditions prevent the parasite from obtaining its own food, or under food stress due to provisioning during the breeding season. Eg. Food shortage during winter months.

Empirical research on gulls has demonstrated that kleptoparasitism is a facultative behavioural strategy that is applied flexibly as ecological conditions vary. Field research conducted by Maniscalco and Ostrand (1997) found that the degree of kleptoparasitism observed co-varies with the concentration of hosts to parasitize (Brockmann & Barnard's (1979) first condition listed in Table 2.2). They found that in mixed-species foraging aggregations of seabirds the rate of kleptoparasitism committed by gulls increased as the density of birds in foraging flocks got higher. So, kleptoparasitism was prompted by changing social pressures mediated by other environmental factors, such as where and how food sources aggregate.

The logic of the above finding has also been demonstrated theoretically in a model developed by Hamilton (2002). Hamilton (2002) used modelling simulations to assess the distribution of foragers between patches that were high or low in the rate of food input, when those foragers differed in competitive ability. Hamilton's (2002) model foragers differed in their efficiency at searching for food and in fighting ability. The model showed that less kleptoparasitism occurred in high resource input patches and that kleptoparasitism increased with decreasing resource input. Increasing the density of competitors in a patch also had the effect of increasing the proportion of kleptoparasites, in line with the observations of Maniscalco and Ostrand (1997). This is likely because increasing the number of

competitors is similar to decreasing resources, as both increase the amount of resource competition being experienced.

The above examples (Maniscalco & Ostrand, 1997; Hamilton, 2002) show the power of theoretical models to work in synergy with and confirm the logic of empirical findings. However, despite such research findings permitting us to confidently assert the utility of kleptoparasitism as a flexible behavioural strategy, no research has yet investigated the value of kleptoparasitism when foragers are faced with conditions very different to the environments to which they are adapted. The increasing urbanisation of certain gull populations provides an opportunity to address this question and investigate the role of kleptoparasitism in enabling gull populations to invade these novel spaces.

Research investigating how the use of kleptoparasitism differs between urban environments and the traditional ecologies of gulls and the ecological conditions that best predict these differences will develop our understanding of the importance of kleptoparasitism in extending the range of habitats a kleptoparasitic species can tolerate. Given the increasing conservation priority of certain gull species such knowledge may be invaluable in predicting the population trajectory of this family of birds, and make us better informed about their chances of overcoming their recent decline.

In this section I have outlined research literature, both empirical and theoretical, that shows that kleptoparasitism is a facultative behavioural response applied flexibly by gulls when changing environmental parameters make it a useful strategy (Maniscalco & Ostrand, 1997; Hamilton, 2002). This suggests that kleptoparasitism may play an important role in allowing gulls to meet their energy needs and be successful in the novel urban environments in which they are increasing. However, thus far no research has investigated differences in the use of kleptoparasitism by gulls between novel urban environments and their traditional foraging ecologies, nor looked at the ecological variables that may best predict any differences in kleptoparasitism that may be seen across these environments. The key questions addressed as part of this research aim were:

Key Question 1: Does kleptoparasitism use differ across environments?

Key Question 2: How do ecological variables influence kleptoparasitism?

These two key questions were addressed in Study 1.

2.4 – Research Aim 2: To investigate kleptoparasitic foraging behaviour in competitively asymmetric populations

The dimensions upon which competitive asymmetries between individuals are measured can be continuous (eg. age, size), or discrete (eg. sex, species) (Giraldeau & Beauchamp, 1999), and, as Maynard Smith (1982) has highlighted, the players in the game must be aware of, or able to perceive, the competitive asymmetries between each other in order for those asymmetries to influence their choice of action. Three types of asymmetry have been identified as relevant to social foraging populations (Maynard Smith & Parker, 1976). These are:

- *Asymmetries in payoff* (Broom & Rychtar, 2013) – The gains obtained by some individuals differ from those obtained by other group members. For example, the starvation state of an animal may dictate that a food resource is worth more to that individual than to other group members; or, differences in search and handling efficiency will mean the average rate of intake from a bout of foraging is higher for some group members than others.
- *Resource Holding Potential (RHP)* (Maynard Smith & Parker, 1976) – Relates to differences in various aspects of the phenotype that will affect access to resources. For example, differences in fighting ability will give some individuals priority of access to food, and may be the consequence of traits such as size, weaponry, or age-related developmental differences.
- *Uncorrelated asymmetries* - These are effects that are not the consequence of the first two asymmetries. Asymmetries between individuals will still settle contests over resources even if the resource has the same value for all competitors (Maynard Smith, 1982), and in some cases differences in RHP will have no relevance to the competitive situation. Maynard Smith and Parker (1976) cite the example of differences in arrival at a patch. The first to arrive and a latecomer will clearly have different intake rates that are a consequence of the rate at which the patch has been depleted before the arrival of the second individual. Behaviours that have evolved as a result of social conventions may also reflect uncorrelated payoffs, there may be no difference between individuals in competitive ability, but some convention will influence which individual has priority of access to resources.

Amongst the multi-cellular organisms there will be very few social foraging populations whose members are competitive clones, so all real foraging populations will be asymmetric to some degree. The complexity of interactions in kleptoparasitic populations of foragers who are competitively unequal has meant that there are a number of questions regarding behaviour in such populations that are worthy of further research.

Key Question 3: How do differences in competitive ability influence kleptoparasitic behaviours?

The study populations used in this research, at Brancaster Bay and Billingsgate Market, were mixed-species populations of gulls. Gull species differ in size and therefore differ in agility, strength and competitive ability. These study populations presented an opportunity to investigate how competitive asymmetries between the individuals that compose the population influence the behaviours seen in a population of foraging kleptoparasites.

Previous research has been conducted assessing how kleptoparasitic behaviours differ between species of gulls when they compete for food resources. Verbeek (1977b) investigated species differences in the use of kleptoparasitism between Herring gulls (HG: *Larus argentatus*) and Lesser Black-backed gulls (LBB: *Larus fuscus*), finding that LBB engaged in more kleptoparasitism when the two species competed for food waste at a landfill site in the UK. However, that research did not seek to consider competitive asymmetries between those species as the driver of the behavioural differences seen. The species difference seen in the frequency of kleptoparasitism was attributed to evolved differences in foraging technique as a consequence of lifestyle. The HG as a foreshore specialist could dig through the refuse in search of food in a manner similar to which it might uncover food on a beach. The LBB in contrast, as a pelagic species more known for catching its food out at sea, did not engage in this digging behaviour and instead attempted to steal the food finds of HG's.

A further piece of research that did focus on competitive asymmetries when investigating foraging behaviour in a kleptoparasitic population used a non-avian study species. King, Isaac, and Cowlishaw (2009) examined the social foraging tactics of wild troops of chacma baboons (*Papio ursinus*). Group size in baboon troops can be relatively stable and a baboon troop will range over large areas whilst foraging in isolation from other troops. Kleptoparasitism is a regular foraging strategy for baboons and the members of these species show a great deal of size dimorphism both between and within sexes, making some individuals better competitors and more dominant than others.

As described previously (section 2.3), the model of kleptoparasitism developed by Hamilton (2002) considered a population of foragers that differed in competitive ability. Hamilton (2002) argued that differences in competitive ability will influence a forager's use of kleptoparasitism, with individuals that are more dominant and high in fighting ability making more use of kleptoparasitism. This prediction was supported by the findings of King et al. (2009) in relation to female-female interactions, with high ranking females stealing more from subordinates. However, in relation to female-male interactions they reported that low-ranking females scrounged more from males. It is worthy of note that, on the whole, females scrounged more from males when pregnant or lactating (King et al. 2009), suggesting that these mixed results may reflect a tolerance by males of female scrounging as an indirect form of parental investment or that pregnancy handicaps normal foraging ability.

King et al. (2009) concluded from their study of wild baboons that the dynamics of kleptoparasitic behaviour in their troops were shaped by a complex interaction of social and reproductive factors. This conclusion reflects the fact that baboons are a socially complex primate

with strict dominance hierarchies, and strong social and kinship affiliations which would complicate any analysis of social foraging interactions.

The mixed results reported by King et al. (2009) with regard to the effects of competitive ability and dominance on rate of kleptoparasitism are surprising, as the results of Hamilton's (2002) model demonstrate theoretically that dominant individuals should have priority of access to food items. However, as stated above the complex sociality of baboon troops might explain the King et al. (2009) finding. Further research is clearly needed to understand the effects of differences in competitive ability on kleptoparasitic dynamics in social foraging groups. Studies using wild populations of less socially complex species may provide clarification of this issue. The mixed-species foraging groups of gulls utilised in this research met this criteria and were used to assess how differences in competitive ability influence kleptoparasitic behaviours.

Key Question 4: How does ability to use different types of kleptoparasitism influence the behaviour of kleptoparasites and the responses of hosts?

Competitive asymmetries, as described above, increase the complexity of social foraging interactions, however, real foraging populations can contain additional layers of complexity beyond this. The ability of members of a foraging population to use different types of kleptoparasitic strategy is one area that will add extra dimensions of complexity to research attempts to understand behaviour in competitively asymmetric populations. Consideration of such factors will, however, provide a more realistic representation of the foraging population under investigation.

As discussed in the previous chapter (section 1.2), three types of kleptoparasitism have been described in the literature: aggressive, scramble, and stealth kleptoparasitism (Giraldeau & Caraco, 2000). Many research studies, particularly those using populations of seed feeding passerines as study populations, have focused on scramble kleptoparasitism in isolation. However, Morand-Ferron, Giraldeau, and Lefebvre (2007) investigated kleptoparasitic behaviour in a wild population of a bird species, the Carib grackle (*Quiscalus lugubris*). These researchers used field experiments where free-ranging populations of Carib grackles were provisioned with quantities of food. Each item of food was indivisible and required some handling before it could be exploited. The Carib grackles studied by Morand-Ferron et al. (2007) utilised aggressive and stealth kleptoparasitism to obtain these food items.

Morand-Ferron et al. (2007), found that scrounging was negatively frequency-dependent in line with the predictions of Producer-Scrounger models (section 1.3.3). They also reported that increasing the cost of scrounging resulted in less kleptoparasitism, and increasing the cost of producing resulted in more kleptoparasitism. However, Morrand-Ferron et al. (2007) were able to provide little insight into how the use of different types of kleptoparasitism shaped patterns of behaviour in their study population. This may be because, with only one study species, there was no easy way to discern differences in competitive ability between foragers, so identifying the relationship between how differences in competitive ability influenced the use of different types of kleptoparasitism

may not have been possible. Morand-Ferron et al. (2007) identified this as a neglected area of research and recommend tests of kleptoparasitic models using populations that can utilise the other types of kleptoparasitic strategy that are possible. Mixed-species foraging flocks of gulls provided a good model system for addressing these questions as these species' can use all three of the kleptoparasitism strategies described and differences in competitive ability can also be readily identified through size differences between species and age differences within species that are recognised through plumage.

Key Question 5: Is stealth kleptoparasitism an example of a Marauder strategy (strategy X)?

Maynard Smith (1982) developed a model assessing contests over a resource. In this model competing animals have four strategies available to them. The first two strategies are called *Hawk* and *Dove*. Hawk is an aggressive strategy in which, when an animal encounters an opponent and a resource, it escalates and continues to fight until it wins the resource or is injured and cannot continue fighting. Dove is a passive strategy of bluff in which the animal displays like it is challenging for the resource, but if the opponent escalates the animal backs off immediately, and if the opponent does not escalate the resource is shared between the two opponents after they have finished their ritualised mutual displays. The other two strategies were called *Bourgeois* and *strategy X*. When adopting the Bourgeois strategy an individual will use the Hawk strategy in a contest if they are the owner of the resource, and use the Dove strategy if they are challenging for the resource. Strategy X is the opposite of the Bourgeois strategy, whereby the individual plays Dove if it is the owner of the resource, and uses the Hawk strategy when it is challenging for the resource. Maynard Smith (1982) speculated that such a strategy may reflect situations in nature where a resource is held for a short period of time and decreases in value the longer it has been held. This would fit a foraging context where a food item decreases in value constantly as it is handled, and therefore has a lower value to the owner after it has exploited the item for a while.

Maynard Smith (1982) used the term intruder in relation to being the challenger for a resource, this was because the model was a generalised contest over any valuable resource. So, the resource could be a nest site, territory, control over a mate, or a food item. In-keeping with the central questions of the current research I will discuss the Maynard Smith (1982) model in a foraging context and use the term challenger where Maynard Smith (1982) used intruder.

With the rival foragers in this model population having four strategies from which to choose, including two that are contingent on roles (owner or challenger), this creates an asymmetric game which could be considered to match any of the three types of asymmetry discussed at the start of this section (2.4). Maynard Smith (1982) considered the asymmetry in this model to be an uncorrelated asymmetry but if the differences between the contestants were considered to be of the other two types (asymmetries in payoffs or RHP) qualitatively similar conclusions would follow from the model. Here I consider the asymmetry to be a difference in payoffs.

The key assumptions of the model are that competitors know which role they occupy, as stated previously this is essential if the asymmetries are to influence behaviour. The number of individuals using each strategy is equal in frequency in the starting population. The value to the owner of the food item being contested is denoted by V, and the value of the food item to the challenger is denoted by v, where $V > v$. Table 2.3 shows the payoffs for this model with these resource values. C represents the costs of an escalated fight or contest.

Table 2.3. Payoffs for the asymmetric Hawk-Dove-Bourgeois-X game when the value of the food item differs between the owner (V) and the challenger for a food item (v). Adapted from Maynard Smith (1982). The expressions shown in the below table indicate the payoffs obtained by individuals using one of the four strategies in pairwise contests against opponents who also use those strategies.

	Hawk	**Dove**	**Bourgeois**	**Strategy X**
Hawk	$\frac{1}{4}(V + v - 2C)$	$\frac{1}{4}(V + v)$	$\frac{1}{4}(2V + v - C)$	$\frac{1}{4}(V + 2v - C)$
Dove	0	$\frac{1}{4}(V + v)$	$\frac{V}{4}$	$\frac{v}{4}$
Bourgeois	$\frac{1}{4}(V - C)$	$\frac{1}{4}(2V + v)$	$\frac{V}{2}$	$\frac{1}{4}(V + v - C)$
Strategy X	$\frac{1}{4}(v - C)$	$\frac{1}{4}(V + 2v)$	$\frac{1}{4}(V + v - C)$	$\frac{v}{2}$

For the case above, Maynard Smith (1982) showed that if all four of these strategies are pure strategies (Appendix B) then Bourgeois is an ESS when $V > C$, and Bourgeois and strategy X are ESS's when $V < C$. For mixed strategies the solution changes slightly. If Hawk and Dove are treated as strategies over which competitors can randomise with positive probability, then Bourgeois is still an ESS when $V > C$, and Bourgeois and strategy X are still ESS's when $V < C$. However, strategy X could not invade a population where the use of a mixed strategy of Hawk and Dove was prevalent. If the population was already at a strategy X equilibrium then it would remain stable and could not be invaded by one of the other strategies, but the population could not evolve to a strategy X ESS if lots of foragers were using a Hawk-Dove mixed-strategy.

The model developed by Maynard Smith (1982) shows that asymmetric models can produce counter-intuitive results as their several parameters combine in complex ways. In relation to the solutions described for this particular model it needs to be retained in mind that v (value to the challenger) always has a lower value than V (value to the owner), so to find that strategy X is an ESS when the costs C are greater than even V, is a surprising finding that few people would be able to intuit. Because of this, Maynard Smith (1982) described strategy X as a paradoxical ESS rarely likely to be seen in nature, and actually stated "I know of no example in which contests are won conventionally by the contestant to whom the value of winning would be lower" (Maynard Smith, 1982, p.103).

Broom, Luther, Ruxton and Rychtar (2008) developed a model of kleptoparasitic behaviour in a social foraging population that built on the basic structure of the Maynard Smith (1982) model

described above. Broom et al. (2008) introduced the idea, implicit in the Maynard Smith (1982) model, that there are two sides to a kleptoparasitic interaction, these are the actions of the kleptoparasite and the response of the victim or host that is targeted. At its most basic this interaction can be reduced to four actions. The kleptoparasite will either *attack* or *not attack*, and the host will either *resist* or *not resist*. These options generate four combinations of kleptoparasitic opportunity and threat (attack- resist; attack- not resist; not attack- resist; not attack- not resist) (Broom et al. (2008).

If a focal study of an individual in the population is conducted over a period of foraging this would reveal occasions when they were acting as both a parasite and a host, and thereby reveal a strategy based on the two sides of the kleptoparasitic interaction. Broom et al. (2008) considered a population of four different bird types. A bird's type was determined by its strategy, based on the four combinations of actions shown above. The four types of bird in the foraging population specified for this model, and their strategies were:

Hawk: Always attack, always resist when host.

Dove: Never attack, never resist when host.

Retaliator: Never attack, always resist when host.

Marauder: Always attack, never resist when host.

Parallels between these strategies and the model of Maynard Smith (1982) are immediately apparent. Hawk and Dove are the same as in the original models and need no special explanation, but it can be seen that the Retaliator strategy is qualitatively identical to the Maynard Smith's (1982) Bourgeois strategy. Likewise, the strategy named Marauder by Broom et al. (2008) is identical to what Maynard Smith (1982) called strategy X. In the context of the kleptoparasitism model in which these four types were used, Doves and Retaliators can be classified as producers and Hawks and Marauders can be classified as scroungers.

In their discussion of the model's results Broom et al. (2008) suggest that the Marauder strategy, originally called strategy X by Maynard Smith (1982), may equate to stealth kleptoparasitism, where the kleptoparasite steals food using speed or guile whilst avoiding a protracted aggressive interaction with the host. As stated earlier in this section, Maynard Smith (1982) considered this strategy to be paradoxical and could cite no convincing examples found in nature of when a contest is routinely won by the individual with least to gain.

In an asymmetric population, where foragers are competitively unequal, stealth kleptoparasitism may represent the best tactic available to a subordinate individual. If the tactic is sufficiently low-risk we should expect it to be present as a way for subordinates to compete with stronger individuals. This should occur even if the payoff is on average lower than that achieved by individuals who are able to successfully use the other types of kleptoparasitism. Considering the other side of the kleptoparasitic interaction, subordinate group members may also be unlikely to resist

kleptoparasitic attempts on occasions when they are the hosts. If it can be demonstrated that stealth kleptoparasitism is used by subordinate group members, and these same individuals don't resist when they are hosts, this would suggest that the existence of a Marauder strategy can be confirmed through empirical research using foraging populations where stealth kleptoparasitism is present, and whose group members are asymmetric in terms of RHP. Again, the gull populations that were the focus of this research were used to assess this conjecture of Broom et al. (2008), that Marauder equates to stealth kleptoparasitism, as these species can utilise all three types of kleptoparasitism (Aggressive, Scramble, Stealth) making them a useful model system to investigate the possibility that stealth kleptoparasitism is an example of a Marauder strategy (strategy X).

Summary: Research aim 2 sought to investigate kleptoparasitic behaviour in competitively asymmetric social foraging populations. This aim was pursued through three key questions (Key Questions 3, 4, 5) as outlined above. The first investigated how differences in competitive ability influenced kleptoparasitic behaviours and the second built on this by assessing how the ability to use different types of kleptoparasitic strategy influenced behaviour in the study populations used. The third question attempted to provide an empirical validation of the suggestion by Broom et al. (2008) that stealth kleptoparasitism equates to a Marauder strategy or what Maynard Smith (1982) called strategy X. These three questions were addressed through study 2 as summarised in Table 2.1.

2.5 – Research Aim 3: An examination of the foraging behaviours used by subordinate individuals in mixed-species social groups

The behavioural strategies utilised by an animal foraging in a group will be influenced by the size of the group, the density of the group in relation to its food source and the ability of the animal to compete with other group members. This last factor makes mixed-species foraging groups an interesting biological phenomenon.

The kleptoparasitic strategies considered so far in this thesis can be effective behaviours in allowing an individual to meet its energy needs efficiently. However, the ability to make effective use of those strategies is contingent on the individual's competitive ability relative to the other foragers in the population. This raises the question of what other strategies might be used by a forager to compete for resources if it is competitively subordinate and unable to make use of kleptoparasitic behaviours against its competitors.

Previous research has reported how differences in size and age affect competitive ability and influence the behavioural strategies that individuals within a foraging group will use. Research by Hansen (1986) used observations of kleptoparasitic behaviour in wild foraging populations of bald eagles (*Haliaeetus leucocephalus*) competing over salmon carcasses. Birds of this species differ in competitive ability based on RHP (size, age and sex), and can also have asymmetric payoffs (hunger level).

Hansen (1986) noted that smaller birds produced more and larger birds made more use of kleptoparasitism. If a forager is more dominant and better at fighting than the other individuals in its foraging group, then, logically, the most efficient way for it to meet its energy needs is to steal from other group members and save itself the full cost of finding its own food. This is in line with dominance predictions discussed previously in relation to the research of King et al. (2009). Juvenile birds, and sub-adult birds were also noted to spend more time searching for food. This last finding suggests payoff asymmetries may be a consequence of developmental differences in foraging ability. If foraging skill develops with age in this species, juvenile birds may have had to compensate for their poor foraging and competitive abilities by spending more time foraging.

A model proposed by Holmgren (1995) also considered how subordinate foragers in competitively asymmetric populations may distribute themselves whilst foraging. Assumptions of the Holmgren (1995) model were that individuals differed in fighting ability, and were categorised as either low or high in fighting ability. The results of the Holmgren (1995) model showed that individuals who were high in fighting ability were more likely to engage in kleptoparasitism, as demonstrated by Hansen (1986), they were also more likely to be found in patches with high food input. This would logically suggest that subordinate individuals who, through their lower fighting ability, were less able to make successful use of kleptoparasitism moved to lower quality patches to avoid having their food items stolen by other foragers.

Research by Barnard and Thompson (1985) has also considered how subordinate foragers in kleptoparasitic populations may adopt behaviours to compensate for their lower status. Barnard and Thompson (1985) studied the behavioural interactions of mixed-species feeding flocks consisting of Black-headed gulls (BHG: *Chroicocephalus ridibundus*), lapwings (*Vanellus vanellus*) and golden plovers (*Pluvialis apricaria*) on meadows and farm fields in the UK. BHG in these populations steal food items from the other species and Barnard and Thompson (1985) found that when BHG were present in foraging patches the other species shifted their selection of prey items. When BHG were present the other species shifted from foraging for large worms, which take longer to extract from the ground and handle giving BHG the opportunity to steal these items, to intermediate sized worms which increased the finder's advantage and gave lapwings and plovers the opportunity to consume more of the worm before the arrival of a BHG kleptoparasite. This provides a clear demonstration of the way foragers may compensate behaviourally for their subordinate status.

Within the asymmetric mixed-species foraging groups of gulls that were the focus of this thesis individuals differed in size, age and foraging skill, and this influenced ability to compete with other group members. These differences made some individuals more dominant and some individuals subordinate within the population and this affected priority of access to resources (Barta & Giraldeau, 1998). Investigating the ways in which subordinate individuals in these groups adjusted their behaviour when foraging socially alongside more dominant individuals was essential to developing a full picture of foraging behaviour in competitively asymmetric populations. The question addressed for this research aim was:

Key Question 6: Beyond kleptoparasitism what behavioural strategies do subordinate foragers use to compete for resources?

This question was addressed in study 3.

2.6 – Research Aim 4: To develop a game-theoretical kleptoparasitism model of a wild population of gulls

Theoretical models form a core part of social foraging research. Foraging models are quantitative research hypotheses expressed using algebraic notation (Milinski & Parker, 1991). As quantitative representations of real systems (Railsback & Grimm, 2012), models must make simplifying assumptions that hold certain aspects of the system constant to test the effect of varying other aspects of the system under investigation. As such, no single model is likely to capture the total complexity of real foraging situations.

Despite these limitations, some of the research discussed in the previous sections (Hamilton, 2002; Holmgren, 1995 – sections 2.3 and 2.5) demonstrated how theoretical modelling can play a powerful role in helping to build theory and explore the kleptoparasitic behaviour of foragers in a systematic and logical way. This is commonly achieved, following the guidance of Stephens and Krebs (1986), by changing one aspect or constraint of the model at a time and investigating the effect this has on foraging behaviour. Real foraging behaviour, using wild or captive populations, can then be compared with the predictions of theoretical models because empirical studies and theoretical models are intended to be synergistic partners in social foraging theory research.

In reality it is extremely difficult to identify populations of animals whose behaviour conforms to all the simplifying assumptions necessary to be tested against a theoretical model. As a consequence the interaction between empirical and theoretical work has been slow and disjointed, so progress has to some extent lacked synergy. This is particularly true when attempting to compare the results of theoretical models against the foraging behaviour of wild populations of animals. As described in the previous chapter (sections 1.2 and 1.3), research into kleptoparasitism concentrates on a number of issues, these are: the conditions that promote kleptoparasitism, the strategies used to carry out kleptoparasitism and the evolutionarily stable frequency of scrounging (kleptoparasitism) to producing. Any theoretical model that considers such factors must make a number of simplifying assumptions, one such assumption is that the size and membership of the population is fixed. This is a hard assumption to meet in wild populations where individuals can leave and arrive relatively freely.

Often a given study species matches a few model parameters making it suitable for a consideration of only one or two predictions generated by a model. For example, the difficulty in finding wild populations to test against theoretical models is highlighted in the research conducted by Hansen (1986) on bald eagles (section 2.5). Due to the complex mix of asymmetries in RHP and payoffs found between individuals in bald eagle populations and the fluid nature of eagle aggregations, Hansen (1986) recognised that a mathematical analysis of the evolutionarily stable

strategies present in the population would be difficult to achieve, so instead used a qualitative assessment of the extent to which behaviour conformed to game theoretic predictions.

Hansen (1986) reported some interesting results. The payoffs for producers and scroungers were calculated by dividing the total food intake obtained through each tactic by the time spent engaged in searching and consumption for each tactic. The frequency of each strategy in the population was approximately 50% and there was no significant difference between the intake rates of both strategies. This suggests that the population had settled at an equilibrium for each strategy and was evolutionarily stable.

The Hansen (1986) study demonstrated that useful insights into kleptoparasitic behaviour can be obtained using wild populations. These insights could check or validate some assumption of a theoretical model or, in the Hansen (1986) case, be used to make a general comparison against game-theoretical ideas. However, a quantitative mathematical confirmation of the findings of Hansen (1986) was not possible, this raises the question of whether it is possible to test a comprehensive model of kleptoparasitism against the behaviour of a wild population particularly when conducting research on highly mobile species such as the gulls that were the focus of this thesis.

Over the past forty years, research into kleptoparasitism using gull populations as a model system has addressed a variety of issues. These include extensive research into the effects of kleptoparasitism on the fitness of host, or victim, species. This has often been assessed through the impact of kleptoparsitism on the breeding success of the host species, studied using species' that nest in colonies (Martinez-Abrain et al. 2003; Quintana & Yorio, 1999). Research by Thompson (1986) and Barnard and Thompson (1985) reversed this focus by assessing the value of kleptoparasitism to the parasite. These researchers analysed the optimality of the parasites' use of kleptoparasitism, finding that BHG targeted food items of optimal size in terms of energy obtained and pursuit costs when stealing food from lapwings (*Vanellus vanellus*) and golden plovers (*Pluvialis apricaria*).

Further, research studies by Verbeek (1977a, 1977b) used gull populations to examine differences in kleptoparasitic foraging behaviour between species (Verbeek, 1977b), as mentioned previously (section 2.4), and between age-classes of gull (Verbeek, 1977a). What these examples (Thompson, 1986; Barnard & Thompson, 1985; Verbeek, 1977a, 1977b) illustrate is that gull species have been used to successfully investigate kleptoparasitic behaviours through research utilising wild populations. This stands to reason as gulls do very poorly in captivity, and there are few, if any, aviary populations. So, behavioural research involving gulls, on the whole, requires observing birds in the wild. A consequence of only being able to use wild study populations has meant there have been no significant tests of theoretical models of kleptoparasitism using gull populations and the studies mentioned here did not incorporate game-theoretic analyses as part of their research approach, this is an area in need of further investigation.

As stated in chapter 1 (section 1.3.4) the kleptoparasitism models developed by Broom and colleagues (Broom & Ruxton, 1998; Broom & Ruxton, 2003; Broom, Luther & Broom, 2004; Broom &

Rychtar, 2007; Broom & Rychtar, 2009; Hadjichrysanthou & Broom, 2012) represent a valuable theoretical contribution to the investigation of kleptoparasitism, however, no empirical attempts have been made to test this modelling approach against the foraging behaviour of real animals. In the research conducted for this thesis I adopted the modelling approach developed by Broom and colleagues as a means of investigating the kleptoparasitic behaviours of a real population of gulls foraging in an urban environment.

This approach was used because it not only allowed me to consider the stable equilibrium frequency of kleptoparasites (scroungers) to hosts (producers) but also permitted an assessment of the optimality of individual foraging decisions at different environmental parameters, in a population that could use all of the kleptoparasitic strategies previously described (aggressive, stealth and scramble). The key questions addressed as part of this research aim were:

Key Question 7: Is the density of producers to scroungers in the population at an equilibrium?

Key Question 8: Does kleptoparasitic behaviour match the ESS predictions for the environmental conditions encountered?

These two questions were addressed in study 4.

2.7 – Summary

In this chapter I have described the four main research aims for this thesis and reviewed the literature of most relevance to each of those aims. The research aims, key questions relevant to each aim and the four studies conducted for this thesis are summarised in Table 2.2.

The first research aim was to assess the role of kleptoparasitism in helping gull species invade novel environments. This was addressed through study 1 which tackled two questions: Does kleptoparasitism use differ across environments? How do ecological variables influence kleptoparasitism?

The second research aim sought to investigate kleptoparasitic foraging behaviour in competitively asymmetric populations. This aim was addressed through study 2. The analyses conducted for study 2 answered the three key questions outlined for that research aim: How do differences in competitive ability influence kleptoparasitic behaviours? How does ability to use different types of kleptoparasitism influence the behaviour of kleptoparasites and the responses of hosts? And, is stealth kleptoparasitism an example of a Marauder strategy (strategy X)?

The third research aim examined the behaviours used by subordinate foragers to compete for resources. This research aim was addressed through study 3, which investigated the key question: Beyond kleptoparasitism what behavioural strategies do subordinate foragers use to compete for resources?

The fourth research aim was to develop a game-theoretical model of the kleptoparasitic foraging behaviours of a wild population of gulls. The purpose of this study was to make significant contributions to the social foraging literature by testing the modelling approach developed by Broom and colleagues (Broom & Ruxton, 1998; Broom, Luther & Ruxton, 2004) against the real foraging behaviour of a wild population of gulls.

In the next chapter I will go on to describe the study sites and populations used in this research in more detail. I will also outline the methods used to obtain the field data on kleptoparasitism that was analysed in this thesis.

(3)

Chapter 3 – Study sites, study populations and fieldwork methods

3.1 – Introduction

In the previous chapter I outlined four general research aims and the four research studies that were conducted for this thesis. I also made brief mention of the locations where research was conducted. In this chapter I move on to describe in more detail the study sites and study populations that were used, as well as the fieldwork methods that were used to study kleptoparasitism in these populations.

3.2 – Study sites

Research was conducted at two UK study sites between July 2014 and June 2015. Three days of observations were conducted at each site in most calendar months. The study sites differed considerably in terms of their ecology.

3.2.1 – Brancaster: Site 1 was a coastal location at Brancaster Beach, Norfolk (Lat: 52°58'30.40"N; Long: 0°38'11.60"E). Brancaster is a public beach, managed by the National Trust, and located on the North Norfolk coastline. The beach is situated within a coastal saltmarsh environment, which, at high tide, results in the tidal flooding of inland areas beyond what would typically make up the beach and foreshore area. Conversely the low tide at Brancaster exposes a large area of sand beach where numerous wader and seabird species aggregate to forage, exploiting food sources such as fish, crustaceans and various marine invertebrates trapped and exposed by the receding tide or corralled into shallow water channels created by the tide draining from the saltmarsh. Brancaster is a natural food web as the ecology consists of several trophic levels, and the food sources at this location are species that mostly occur naturally in this habitat.

The study area at Brancaster was a section of beach demarcated by two natural boundaries. These were water channels where the outflow of water draining from the saltmarsh joins the sea. These two channels marked the east and west boundaries of the study area respectively. At its maximum, when the tide was at its lowest point, the study area covered 1.6 square kilometres. This area was calculated using scaled aerial photographs from google maps (The calculations for the area of the site are attached at Appendix D). Figure 3.1 shows a photo of the Brancaster study site at low tide. It can be seen that this is a flat sand beach with few undulations and dunes. The flatness of the land in this area is one of the reasons the tide goes inland beyond the beach, creating the saltmarshes and the considerable contrast in distance between high and low tides. Figure 3.2 shows an aerial photograph highlighting the study area with boundaries marked.

Figure 3.1. Brancaster study site at low tide.

Figure 3.2. Site 1 Brancaster Beach. Boundaries of the study area are outlined in black. Distance from west boundary of study area (marked zero) to east boundary of study area 2.20km (2200m). Image taken from Google maps 24/11/15.

3.2.2 – Billingsgate: Site 2 was an urban location at Billingsgate Market, London (Lat: 51°30'20.40"N; Long: 0°00'43.90"W). This is a seafood market, operated by the City of London Corporation, in the Canary Wharf area of East London. This is a former dockland area situated in the Thames Estuary that was involved in various forms of ship and cargo trade (including foodstuffs) for several centuries until the late 20th Century.

The food sources at this location result from anthropogenic activities, and as such no natural food web exists. Research at this location was conducted in a car park area used by fishmongers to process and load their stock onto vans, called the Trader's Car Park. The main food sources are seafood waste and leftovers discarded in the car park. The Trader's Car Park covered an area of 0.0104 square kilometres (10,400m^2). The size of this area was calculated using scaled aerial photographs from google maps (Area calculations are contained in Appendix D). Figure 3.3 shows a photograph of the study site. Figure 3.4 shows the boundaries of the Trader's Car Park from an aerial position.

Figure 3.3. Billingsgate study site (area shown is the Trader's Car Park).

Figure 3.4. Site 2 Trader's Car Park, Billingsgate Market. Boundaries of study area are outlined in black. Distances are shown in metres. Image taken from Google maps 24/11/15.

3.3 – Study Species

Gulls were chosen as the study species for this project as they invest heavily in kleptoparasitic behaviours, as discussed in chapter 1 (section 1.4). The kleptoparasitic interactions of interest were gulls stealing from other gulls, making the focal study populations mixed-species flock of gulls in which all group members are able to make use of kleptoparasitic strategies.

Gull species differ considerably in morphology and potentially thereby in aggressive and interspecific competitive ability. Amongst the UK population of gulls some of the most common species are the Great black-backed gull (GBB: *Larus marinus*), Herring gull (HG: *Larus argentatus*), Black-headed gull (BHG: *Chroicocephalus ridibundus*), and Common gull (CG: *Larus canus*). GBB and HG are amongst the largest of gull species, being both predatory and aggressive with large powerful bills. The BHG and CG are, in contrast, much smaller gulls. The BHG in particular has a slender bill, being of similar size to some of the prey species taken by the larger gull species. These species are frequently found together in mixed-species foraging groups. Figure 3.5 shows images of these four species being handled by the researcher, this gives an impression of the relative size differences of each species. Differences in body size in these species are indicators of differences in competitive ability. The GBB and HG being larger are potentially able to dominate resources at the expense of the smaller gulls. This aligns with an aim of this research, to investigate the use of kleptoparasitism in competitively asymmetric populations.

3.3.1 – Gulls at Brancaster: Large numbers of gulls aggregate to forage in mixed species groups on the beach at Brancaster. Although there are unlikely to be any pristine habitats that reflect ideally the environmental conditions in which a species evolved (Schroeder, Nakagawa, & Hinsch, 2011), the

habitat at Brancaster is likely to be similar to the type of shoreline foraging ecology encountered by gulls throughout much of their evolutionary history. Foraging populations of gulls are likely to have been present on this shoreline for a considerable length of time.

Gull foraging at Brancaster covers a period of about four hours, two hours either side of the low tide mark. The most notable gull species present at this site are GBB, HG, CG, and BHG. These four species were the focus of research at Brancaster. All four species are present on the beach throughout the year. However, the numbers of CG and BHG decline over the summer months (between May and July) as large numbers of breeding adults from these species migrate north and east respectively to breeding grounds in other parts of the UK and Europe. The foraging population of gulls at Brancaster, over the year of research, had a mean daily population size of 176 (Range: 0; 924) gulls. The daily mean number of each species at the site was: HG 75 birds, BHG 64 birds, CG 31 birds, and GBB 6 birds. This gives an average population composition of: HG 42%, BHG 37%, CG 18%, and GBB 3%.

3.3.2 – Gulls at Billingsgate: Gulls aggregate at Billingsgate to exploit seafood waste and leftovers discarded in the car park areas. The population of gulls found at this site consists of GBB, HG and BHG. The exact history of the presence of a foraging gull population at Billingsgate is unknown, however, the site has been operating as a fish market in its current location since 1982. It is likely that gulls have been exploiting resources at this site for much of this time. The only other species that occasionally exploit food opportunities at this site are small numbers of visitors from the *Corvidae* and *Columbidae* bird families. However, these species are infrequent visitors that largely avoid foraging groups of gulls.

GBB and HG are present at Billingsgate all year round, with some birds nesting on the surrounding market buildings to breed, however, BHG were largely absent from the site between the months of April and July when they migrated to breeding colonies. The few BHG's seen at Billingsgate during this summer period were juvenile non-breeding birds. The foraging population at Billingsgate had a mean daily population size of 40 (Range: 24, 79) gulls. This mean number of each species making up this daily population was: HG 28 birds, BHG 7 birds, GBB 4 birds, giving a population composition of about: HG 70%, BHG 19%, GBB 11%.

Figure 3.5. The four study species (Clockwise from top left: HG, BHG, GBB, and CG). Dimensions: The researcher's hand is ~90mm from knuckle on the index finger to knuckle of the little finger. Differences in size, reflective of competitive ability, between species are evident from comparison of these photos.

3.4 – Measures

The following measures were recorded at both study sites:

3.4.1 – Population size and composition: The sizes of the populations were calculated using scan samples at 30 minute intervals. The number of gulls at the site, their species and ages were recorded. As gulls have a complex moult pattern that occurs over a number of years as they mature, they can be difficult to age accurately in the field or using photographic images (Monaghan & Duncan, 1979; Grant 1982). For this reason birds were categorised into one of three age classes based on their plumage: juvenile (gulls showing mostly brown feathers), sub-adult (gulls showing a mixture of brown feathers and adult plumage), or adult (gulls showing mostly or entirely adult plumage). As BHG reach mature plumage in their second year birds of this species were classified using only the juvenile and adult age classes (Svensson, Mularney & Zetterstrom, 2009). Appendix E shows images depicting these three plumage categories.

3.4.2 – Kleptoparasitism: Kleptoparasitism was recorded as frequency counts, and all kleptoparasitic attempts, both successful and unsuccessful, were counted. Kleptoparasitic behaviours were deemed to have taken place if any of the three strategies of aggressive, stealth, or scramble kleptoparasitism described by Giraldeau and Caraco (2000), were used. These were operationalised as follows:

3.4.2.1 – Aggressive kleptoparasitism: the use of force or threat to obtain exclusive control over a resource.

Aggressive kleptoparasitism occurred if the parasite used force or threats to attempt kleptoparasitism through any of the behaviours described in Table 3.1. The use of threats constituted attempted kleptoparasitism without the incident necessarily escalating to physical contact between the parasite and the host, as the host could choose to surrender the food item rather than defend it. Successful use of aggressive kleptoparasitism occurred only if the parasite obtained the whole of the food item being contested, either by physically taking it or if the host surrendered the item following one of the threats described.

Table 3.1. Behaviours constituting strategies of aggressive, stealth, and scramble

Strategy		Behaviour
Aggressive	Force	Kleptoparasite uses of bill to make contact with host's body in order to effect theft.
		Attempt to physically pull or tear food item from host.
	Threat	*Upright threat posture* – Bird stands upright with head tilted forward, and holds wings out from body so they are clearly defined and no longer partly-concealed by the contour feathers of mantle and body (Tinbergen, 1953).
		Wings spread – Kleptoparasite charges the host with wings spread.
		Charge – (BHG only) Kleptoparasite drops its head forward, flattens out its body and then charges at the host.
Stealth		Food stolen from the floor in front of the host.
		Food stolen whilst the host is distracted and not in contact with the food item.
Scramble		Two or more gulls simultaneously attempt to steal portions of the host's food item.

3.4.2.2 – Stealth kleptoparasitism: The use of kleptoparasitism to take food items while avoiding interactions with the host.

Stealth kleptoparasitism was usually typified by the use of speed to approach, grab the food item, and leave without the host noticing, with no physical contact between the two birds. Behaviours constituting stealth kleptoparasitism are described in Table 3.1. If the parasite managed to obtain any proportion of the food item being contested successful use of stealth kleptoparasitism had occurred.

3.4.2.3 – Scramble kleptoparasitism: When a food item is simultaneously exploited by two or more competitors.

For an interaction to be considered scramble kleptoparasitism, there first had to be a food item that was in the possession of one individual. This condition was necessary to avoid confusion with *scramble competition* which is common amongst gulls. Scramble competition occurs when a group of birds rapidly deplete a resource in a feeding frenzy. If the items being contested had no clear owner then this was considered to be scramble competition, however, if a gull was in possession of a food item and it was approached by multiple gulls that simultaneously attempted kleptoparasitism, this was classed as an occurrence of scramble kleptoparasitism. Successful scramble kleptoparasitism occurred if two or more individuals simultaneously acquired portions of the host's food (Table 3.1).

3.4.3 – Prey Size estimates: Size of food items was estimated visually using a measure of bill lengths. As all four study species differ in size and bill length a standard measure was needed to estimate the size of a food item in the field. This standard measure was calculated as described in Table 3.2. The HG bill length was used as a standard measurement to assess the length of a food item. This meant a BHG or CG contesting a food item about 1.5 times its bill length would receive a length score of 1 bill

length, and an item the size of a BHG/ CG bill would be classed as less than 1 bill length. Conversely, a GBB holding an item the length of its bill would be given a score of greater than 1 bill length.

Table 3.2. Data used to obtain a standardised bill length measurement in millimetres.
Calculated by taking the average bill length (BL) in millimetres (mm) for each species (for both males and females) obtained from Malling Olsen and Larsson (2003), and then taking the mean of all four species' means. This averaging across species returned a figure of 45mm. This was closest to the HG bill length with a difference of 7mm. The HG bill length was therefore used to assess the size of a food item in the field.

Species	Mean BL (male)	Mean BL (female)	Species mean BL	45mm - Species mean BL
CG	36.10	32.70	34.40	11
BHG	33.60	31.60	32.60	12
HG	55.20	49.70	52.45	7
GBB	63.10	57.60	60.35	15
		Standardised BL:	**45mm**	

3.4.4 – Ancillary data: Weather conditions and tide levels were recorded for each field session. Wind speed and temperature were measured using a handheld anemometer manufactured by ClimeMET (model CM2030). Wind direction was recorded using a handheld field spotting compass. Light levels were measured using a Digital Instruments (model LX1010B) lux meter. Weather conditions were recorded at the start of each field session, and in some cases further recordings were taken if the prevailing weather conditions changed significantly. Tide levels were assessed on a six-and-a-half-hour tidal cycle, with a two-hour period either side of high tide being classed as high tide levels, two-hour periods either side of the low tide mark being classed as low tide, and the intervening two hour periods between high and low (tide going out), and low and high (tide coming in) being classed as mid tide.

3.5 – Procedure

3.5.1 – Brancaster: Observations were conducted across all tide levels to assess the presence and amount of foraging at different tide heights. The time when the largest numbers of birds were present on the beach was at low tide. As a result the majority of field sessions were conducted during the low tide period, this included sessions before and after the tide reached its lowest point. Field sessions had a mean duration of 2 hours (Range: 1h 30m – 3h 40m), and a total of 74 hours 28 minutes of observations were conducted at Brancaster over 34 field days. Field sessions were conducted during the hours of daylight, between 04:45 hours and 17:00 hours, to permit behaviour to be filmed.

Observations involved the researcher scanning the beach for groups of gulls and then approaching to within a distance from which foraging patches could be identified and filmed. Patches were classified as discrete clusters of two or more birds exploiting a food source or searching for food in a given area. Once a patch was identified, filming was carried out from a fixed position with the

camcorder mounted on a tripod. The distance from which a patch was filmed varied from patch to patch and was contingent on how close the researcher could approach without disrupting the foraging birds. As flight distance is likely to vary between birds and patches the distance from which a patch was filmed was based on the subjective assessment of how close the researcher felt they could get without disrupting foragers. Patches were filmed using a Sony 8.9 megapixel HD camcorder. Recording of a patch was concluded when the food source was depleted and the gulls in that patch dispersed. The duration of patches recorded ranged from 0 minutes 32 seconds to 40 minutes 47 seconds, and 142 patches were recorded over the year of study. The location of the patch on the beach was recorded, along with the start and end time of the patch and a headcount of gulls making up the patch. An example of the datasheet used to record patches is attached at Appendix F. Patch videos were analysed at a later time for kleptoparasitic incidents. This field procedure required considerable movement by the researcher around the study area, and frequent scanning of the beach using binoculars (Viking 10x42) to identify and approach aggregations of gulls.

Headcounts were conducted every 30 minutes from the start of a field session, by taking headcount photos from wherever in the study area the researcher happened to be at the time the headcount was due. This was dictated by the location of foraging patches, so it was not possible to take headcount photos from one fixed position on the beach. To record headcounts a series of photos of the beach was taken, using a Nikon Coolpix P510 (42x zoom) bridge camera, to capture all gulls in the study area. These photos were analysed at a later time to calculate the population size and composition.

3.5.2 – Billingsgate: Observations at Billingsgate were conducted between the hours of 7am and 3pm. The trading hours for the market are 3am to 8:30am. After 8:30am the main activity at the site is the clean-up of the market and car park areas. Prior to 7am it was not possible to conduct observations as the large number of vehicles at the site made unobstructed observations of the study area unfeasible. After 7am the car park emptied considerably making it easier to conduct observations. This was the time that the largest number of gulls forage in the car park. Field sessions were conducted on days when the market was operational (Tuesday – Saturday) and when it was closed (Sunday, Monday).

Observations were conducted from a vehicle. On each study day the location that would give the best unobstructed view of the study area was identified and used as the observation position for that field session. It was not always possible to use the same position as the unpredictable nature of vehicular traffic at the site meant a good observation point one day may have a view obstructed by a large vehicle the next. Filming of foraging patches was conducted from inside the vehicle. Using the vehicle as a hide in this way meant that the presence of the researcher did not disturb foraging behaviour in the study area. Patches were filmed until the resource in the patch had depleted and the birds dispersed. Over the year of study 183 foraging patches were recorded and these ranged in duration from 0 minutes 25 seconds to 29 minutes 36 seconds. The location of patches within the

study area, the start and end time of the patch and the headcount, species and ages of the gulls present at the patch were recorded. An example of the datasheets used is attached at Appendix G. Patch videos were analysed at a later time for kleptoparasitic incidents. Patch videos for Billingsgate were also analysed to assess foraging rate at the site. This involved counting all occasions when foragers in a patch sampled the ground for a food item, and all occasions when they actually obtained a food item.

Headcounts were conducted at 30 minute intervals from the start of a field session. As with Brancaster, a series of photographs was taken of the study area, and later analysed to calculate the population at the time of the sample, including the species and ages of the gulls present. The same recording and photographic equipment used at Brancaster was utilised at Billingsgate.

3.5.3 – Field experiment at Billingsgate: An additional piece of fieldwork was conducted at Billingsgate. After observations of natural foraging behaviour had been concluded at Billingsgate, a field experiment was conducted for one hour, where food was provisioned for the gull population to exploit. Twenty food items of known sizes and calorific values were distributed in and around a pen style enclosure as depicted in Figure 3.6. Food items were placed in the same configuration on every occasion, and all items were ranked based on their size and energy content. The enclosure provided two environments for the gulls to navigate when foraging. The food distributed outside the enclosure could be accessed by landing near or approaching food items. To access food items in the enclosure required birds to land inside the pen. The foraging behaviour of gulls was filmed as they exploited these provisioned food items. Recordings were analysed to assess which food items the gulls prioritised and which items were the subject of kleptoparasitic attempts. As with other kleptoparasitic interactions, the species and age of the parasite and host were recorded as well as the kleptoparasitic strategy used. The size and calorie ranking of the food item being contested were also recorded. Appendix H shows an example of the datasheet used in the field experiment including the values and configuration of food items used in this provisioning study.

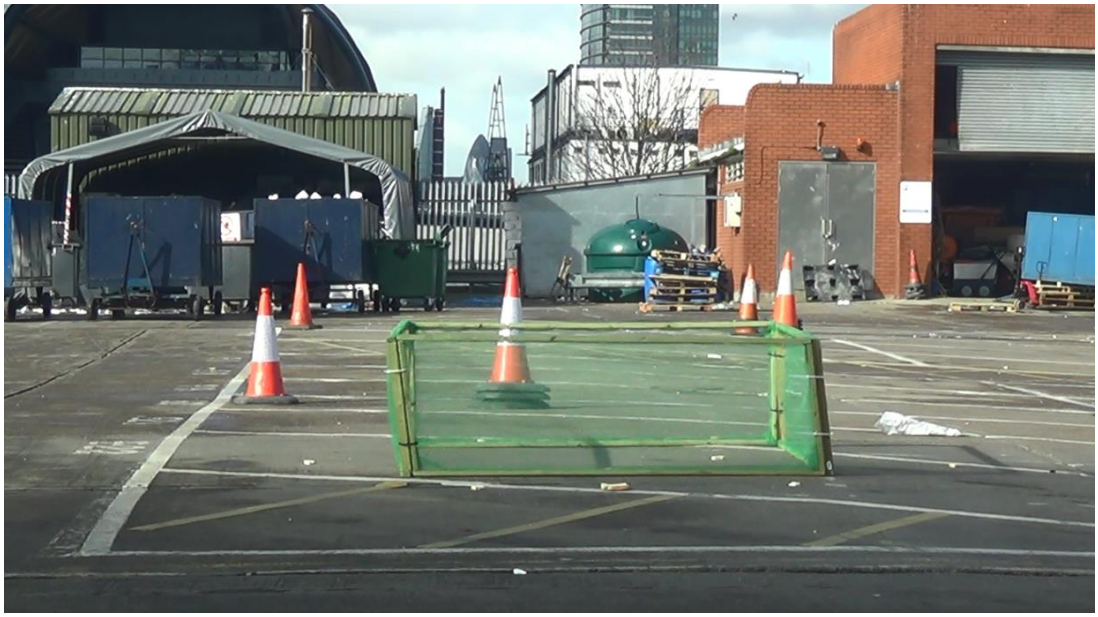


Figure 3.6. Field experiment enclosure. Food items of known sizes and calorific values were provisioned both inside and outside the enclosure to assess which items and locations were prioritised by foraging gulls.

3.6 – Ethics

This research conducted used observational methods to study animal behaviour. All research studies were ethically approved by the Psychology Ethics Committee at Middlesex University. All fieldwork was conducted in accordance with the guidelines for the treatment of animals in behavioural research published by the Association for the Study of Animal Behaviour (ASAB, 2012).

3.7 – Summary

In this chapter I have described the main study sites and study species that were the focus of research for this project. I have also described the various measures that were used, how those measures were constructed, and the procedure by which data was recorded. With these methods described, in the following chapters I will go on to consider each of the four studies making up this thesis by outlining the various analyses that were conducted in order to address each study question, the results obtained for each study before discussing the implications of those results.

(4)

Chapter 4 – Study 1: Kleptoparasitism in gulls at an urban and coastal foraging environment: An assessment of differences in the rate of kleptoparasitism across environments and the ecological predictors of kleptoparasitism

4.1 – Introduction

The previous chapter outlined the field methods that were used to collect data on kleptoparasitism at Brancaster and Billingsgate. In this chapter I will describe how the data were analysed to address the questions that were the focus of study 1. I also present the results of those analyses and discuss the implications of the findings in relation to the predictions made for this study.

4.2 – Study rationale and predictions

A first step towards understanding the role that kleptoparasitism might play in helping species to succeed in novel environments involves assessing how kleptoparasitism differs between environments, and which ecological conditions influence or predict this change. In this study I investigated differences in the rate of kleptoparasitism in foraging gull populations across two environments with contrasting parameters. The first a coastal environment, assumed to be typical of shoreline foraging ecologies encountered by gulls throughout much of their evolutionary history, the second an urban environment. The coastal site was Brancaster Bay, Norfolk, UK, and the urban site was Billingsgate Market, London, UK. The study population at this urban site forage for food waste in the car park areas of a seafood market (see Chapter 3). In addition, in this first study I assessed several ecological variables to see which best predicted any differences in kleptoparasitism observed across the two environments. The ecological variables were: *prey size*, *population density*, *season* and *species of kleptoparasite*.

As outlined in Chapter 2 (section 2.3), kleptoparasitism may be an important foraging strategy that allows gulls to meet their energy needs when changed environmental conditions are encountered. This study addressed the first research aim (Chapter 2, section 2.3) by assessing how the use of kleptoparasitism differs between urban environments and traditional foraging ecologies. It also examined which ecological variables best predict the differences seen in kleptoparasitic behaviour and represented the critical aspects of the environment that promote kleptoparasitism.

The following predictions were made in relation to kleptoparasitic behaviour at the two study sites: 1) that population density would be positively related to the rate of kleptoparasitism, 2) that large prey items would be more susceptible to theft, so that prey size should co-vary with kleptoparasitism rate, 3) that kleptoparasitism would vary between breeding (March to August) and non-breeding

seasons, 4) that gull species would differ in their use of kleptoparasitic behaviour and 5) that there would be a higher rate of kleptoparasitism at the urban site, where food was predicted to be a rapidly decreasing resource.

4.3 – Analyses

Study 1 investigated the two key questions outlined for research aim 1 (see Chapter 2, Table 2.1). As stated above, the first compared the two study environments of Brancaster and Billingsgate to see if there was a difference in the rate at which gulls used kleptoparasitism at those sites. The second assessed which ecological variables were the best predictors of any difference in kleptoparasitism seen between the two sites. The data analysed in this study were kleptoparasitism frequency counts collected for both study sites (Chapter 3, section 3.4.2), data on population composition recorded at Brancaster and Billingsgate (Chapter 3, section 3.4.1), data on prey size estimates (Chapter 3, section 3.4.3) and data on patch duration (Chapter 3, sections 3.5.1 and 3.5.2). The treatment of data, variables considered, and analyses conducted to investigate these two questions are outlined below.

4.3.2 – Population Density: Population density was calculated by dividing the headcount at each patch by the area of the study site (See Appendix D). This produced a measure of birds per kilometre square for each foraging patch. Kilometres squared was used as the unit of measurement because the areas of both sites were large relative to the size of the foraging populations, and using metres squared produced population densities that were numerically extremely small. The use of kilometres squared removed the need for the use of scientific notation, and made the scores more practical for computations.

4.3.3 – Prey Size: Prey Size captured the variation in the size of prey items that were the subject of kleptoparasitic attempts, and was measured on a scale using bill lengths as described in Chapter 3 (section 3.4.3). The assumption was made that as the size of a prey item increases its abundance in the environment on the whole decreases. This was a reasonable assumption to make at Brancaster which is a natural food web with large numbers of small marine invertebrates and fewer larger prey items (Cohen, Jonsson, & Carpenter, 2003; White, Ernest, Kerkoff, & Enquist, 2007). However, it was not apparent that this assumption would necessarily hold at Billingsgate where the food, being anthropogenic waste, may result in the overrepresentation of certain sizes of food item. To check whether the assumption of decreasing abundance with increasing prey size would still hold at Billingsgate it was necessary to check the frequency with which individual prey items of each size occurred at that site. This was achieved by assessing the number of items that had been the subject of the 595 kleptoparasitic incidents at Billingsgate and then assessing their abundance relative to size. To do this prey size was split into four categories: Less than 5 bill lengths, 6-10 bill lengths, 11-15 bill lengths, and greater than 16 bill lengths. It was found that the 595 incidents of kleptoparasitism related to 186 different items of food. When the size and abundance of the 186 items was calculated it was found that 59% of the items fell into the category of less than 5 bill lengths, 28% were 6-10 bill lengths, 8% were 11-15 bill lengths, and 5% were greater than 16 bill lengths, as shown in Figure 4.1.

This indicated that the relationship between and assumption of declining abundance with increasing size of prey items might hold for Billingsgate as well as Brancaster and was a reasonable working assumption to make.

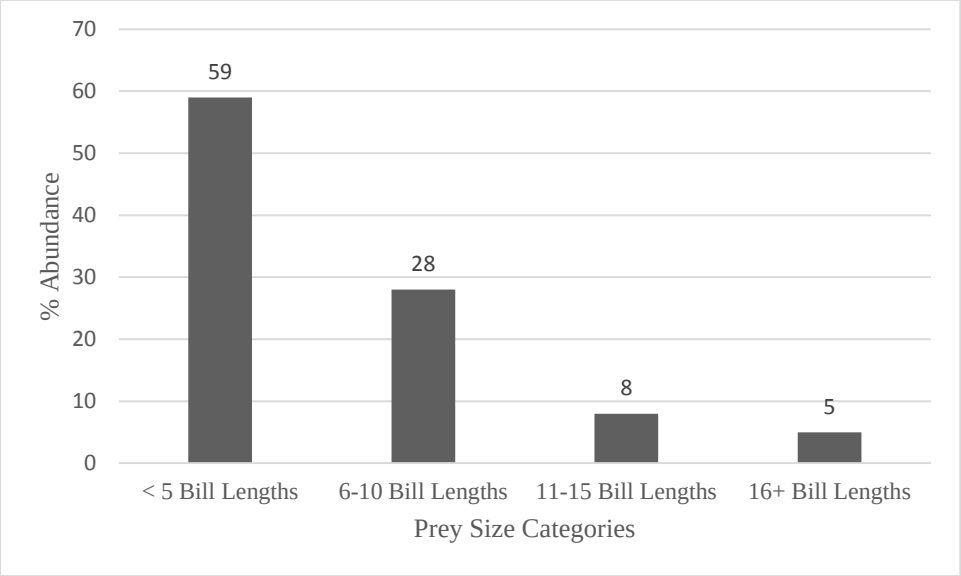


Figure 4.1. Relationship between abundance and size of prey items in the environment at Billingsgate.

For the analyses the original prey size values in bill lengths were used after being converted as follows: an item ≤1/2 bill length was given a value of 0.5; an item <1 was given a value of 0.75; an item x, where 1<x<2, was given a value of 1.25. All other values (1; 2; 3; 4; 5; and 6 bill lengths etc.) were retained as their original integer values.

4.3.4 – Season: Data was collected over a full calendar year at both study sites. To consider whether there may be seasonal differences in the rate at which gulls kleptoparasitize each other, the year of study was dichotomised into two seasons. These were: Breeding (March to August) and Non-breeding (September to February).

4.3.5 – Kleptoparasitism Rate: Measures of patch duration were recorded in minutes. The total number of kleptoparasitic events within a patch divided by patch duration gave the rate of kleptoparasitism (per minute). As patch duration increases we should expect the probability of kleptoparasitism to also increase, as more time gives more opportunity. Calculating rate in this way controlled for those effects.

Each kleptoparasitic event was entered into a dataset such that each line of data included a kleptoparasitism rate for the patch within which the event was observed; a species designation for the kleptoparasite; prey size; population density, recorded at the level of the patch in which the

kleptoparasitic event occurred; a seasonal designation (breeding/non-breeding); and a site designation (Billingsgate/Brancaster). The Brancaster data had one registration removed, as this was for a Lesser Black-backed Gull (*Larus fuscus*); the only one observed in the entire study. This was regarded as a legitimate outlier that would distort subsequent model estimations, if included. In total there were 595 registrations for Billingsgate and 99 for Brancaster after the removal of this outlier.

4.3.6 – Statistical Model: Data were analysed using a series of generalized linear models (GLM). The response variable was the rate of kleptoparasitism (events per minute) for each patch observed. This variable was $\log_n$ transformed to improve the dispersion of data. This response variable was very close to equidispersion (χ2/df=0.945) when entered into an intercept only linear generalized linear model with identity link. The predictor variables were population density (population density for each patch (birds/km^2) over each study area), prey size, season (breeding/non-breeding), species of kleptoparasite (as described in Chapter 3, section 3.3) and site (Billingsgate/Brancaster). The population density, prey size and response variables (section 4.3.5) were each centred and scaled in order to standardize them. Standardizing continuous variables facilitated meaningful comparisons between model coefficients. All statistical analyses were conducted using R version 3.3.1, Generalized Linear Models were generated using the glm() function from the MASS package (R Core Team, 2016). Figures were produced in R using the base package or ggplot2 version 2.1.0 (Wickham, 2009).

4.4 – Results

There were 15 missing data points for prey size and all data associated with these observations were removed from the dataset containing standardized variables. All results are reported on this reduced dataset (Billingsgate (N=593); Brancaster (N=86)).

A series of Generalized Linear Models (N=49), using a Gaussian function with identity link, were developed to investigate the main effects and interactions between the variables: standardised population density, standardised prey size, site, season, species, and the outcome variable standardised kleptoparasitism rate. A sequential approach was taken where predictor variables and interactions were added to the models one at a time. Details of all 49 models are outlined in Appendix L. A main effects model containing all variables (Model 48) indicated that only standardised prey size, standardised population density and site were significant predictors of standardised kleptoparasitism rate. This was the first criterion used for model selection; models containing season and species were eliminated and those containing site, standardised prey size and standardised population density were retained.

Model 48 had an associated Akaike Information Criterion (AICC) value 1473.9. The AICC is a measure of the goodness of fit of a model, normally implemented using a lower is better approach (Zeileis, Kleiber & Jackman, 2008). Models with AICC values which differ by less than 2 are regarded as being similarly good fits, whereas differences in AICC over 2 suggest the model with the higher AICC value is a poorer fit (Burnham & Anderson, 2001). This was the second criterion for model

selection: All models with AICC values greater than that of Model 48 plus 2 (1473.9 + 2) were excluded as they accounted for less information in the data than just putting all variables into the models as main effects. This led to two candidate models (Model 21: AICC 1468.7; Model 37: AICC 1469.3). Model 21 was a main effects model containing site, standardised population density and standardised prey size. All three predictors were significant, with standardised population density and site significant at the p<0.001 level and standardised prey size significant at p=0.01 (See Table 4.1). Model 37 contained main effects and interactions up to and including three-way interactions. The only significant factors were the main effects of standardised population density (p<0.001) and standardised prey size (p=0.01). There were no significant interactions between predictors. This suggested that the more complex model, adding interactions between factors, was no better at accounting for information in the data than the simpler model. On this criterion Model 37 was eliminated and Model 21 retained as the best fitting model.

Table 4.1. Summary of generalised linear models. Exploring the effects on standardised kleptoparasitism rate (events per minute), of site (with Billingsgate as reference), standardised population density, standardised prey size, species of kleptoparasite and season. Model 21 was retained as the best fitting model.

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AICC
21				340.73	675	736.55	1468.7
Constant	0.11 [0.05, 0.16]	0.03	<0.001				
Site	-0.86 [-1.06, -0.66]	0.10	<0.001				
Std Prey	0.08 [0.02, 0.14]	0.03	<0.01				
Std Pop'n	0.46 [0.39, 0.53]	0.03	<0.001				
37				337.01	671	732.37	1469.3
Constant	0.10 [0.04, 0.16]	0.03	<0.001				
Site	0.16 [-70.10, 70.42]	35.85	0.99				
Std Prey	0.08 [0.02, 0.14]	0.03	<0.01				
Std Pop'n	0.44 [0.37, 0.51]	0.04	<0.001				
Site:Prey	0.87 [-69.40, 71.14]	35.85	0.98				
Site:Pop'n	1.26 [-46.70, 49.22]	24.47	0.96				
Prey:Pop'n	0.04 [-0.03, 0.10]	0.03	0.25				
Site:Prey:Pop'n	1.06 [-46.90, 49.01]	24.47	0.97				

As site was a significant predictor of the rate of kleptoparasitism, differences between the two sites were investigated graphically by plotting standardised kleptoparasitism rate against the other two significant predictor variables, population density and prey size, as shown in Figures 4.2 and 4.3. A

positive correlation was apparent between population density and standardised kleptoparasitism rate at Billingsgate, and to a lesser extent at Brancaster (Figure 4.2). A positive correlation was also seen between prey size and standardised kleptoparasitism rate at Billingsgate but this correlation appeared slightly negative at Brancaster (Figure 4.3).

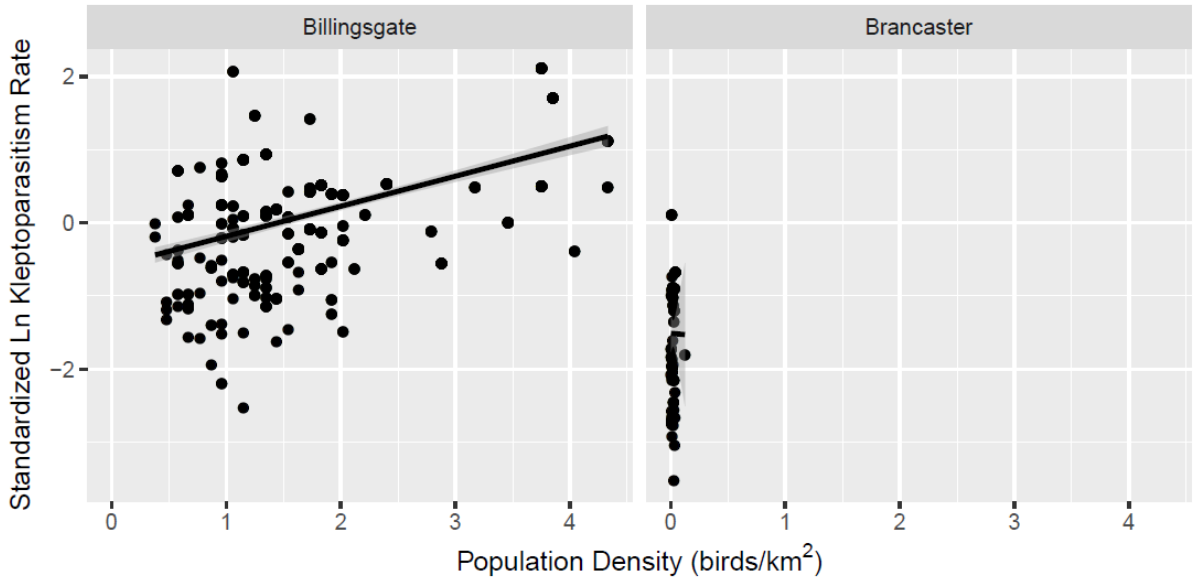


Figure 4.2. Population density plotted against standardized $\log_n$ kleptoparasitism rate. Plots shown for both study sites with fitted regression lines. Shading indicates 95% confidence intervals. Each data point represents the population density per patch.

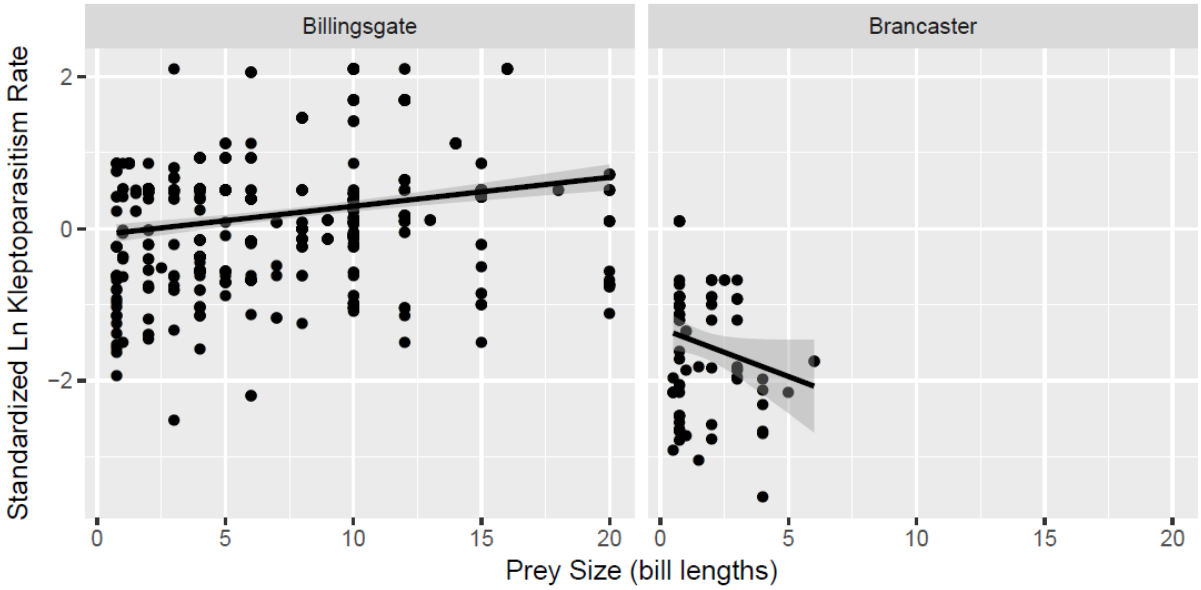


Figure 4.3. Prey size plotted against standardized $\log_n$ kleptoparasitism rate. Plots show data for both sites with fitted regression line. Shading indicates 95% confidence intervals. Each data point plotted represents a different prey item from an event of kleptoparasitism.

Data from Brancaster showed a smaller range of values for prey size and population density than Billingsgate, and in the case of population density the data ranges for the two sites were non-overlapping as shown by the scale of the x axes in Figures 4.2 and 4.3. This suggested that additional data may need to be collected at Brancaster or an equivalent coastal site to capture the influence of these variables on kleptoparasitism across these reduced ranges. Mann Whitney U tests conducted on the data for prey size and population densities between the two study sites confirmed the differences in these two variables between the sites showing that both prey size and population density were significantly greater at Billingsgate as shown in Table 4.2.

Table 4.2. **Differences in prey size (Billingsgate: N = 593; Brancaster: N = 86) and population density (Billingsgate: N = 183; Brancaster: N = 86) between the two study sites.** Differences between sites were tested using Mann-Whitney tests.

Site	Median	Range	Statistic
a) Population density (birds.km^{-2})			
Billingsgate	1.730	0.380 - 4.330	U = 50998, $P < 0.0001$
Brancaster	0.0190	0.0025 - 0.1250	
b) Prey size (bill lengths)			
Billingsgate	8.00	0.75 - 20.00	U = 46575, $P < 0.0001$
Brancaster	0.75	0.50 - 6.00	

The overall finding of a difference between sites was interpreted as a core ecological difference. Both prey size and population density are distributed significantly differently across sites, with Billingsgate having more large prey items and greater population density. Kleptoparasitism rate was higher at the urban study site (Billingsgate), the model that best explained this difference (Model 21, Table 4.1) was a main effects model containing site, population density and prey size. Examination of coefficients indicated that standardised prey size (b = 0.08) was a weak but significant predictor of kleptoparasitism and standardised population density (b = 0.49) was the main driver of the difference in the rate of kleptoparasitism observed between sites.

4.5 – Discussion

The results showed that rates of kleptoparasitism in gulls were affected by bird population density and prey size. While these two predictors seem to be positively correlated with increased rates of kleptoparasitism, differences between the sites in the predictors and the response variable support a more cautious interpretation. It is possible that the population density measure may under-estimate the search time required by would-be kleptoparasites at Brancaster, in contrast to Billingsgate.

Maniscalco & Ostrand (1997) demonstrated how a shift in the foraging conditions in a single environment resulted in an increase in kleptoparasitic behaviour by gulls. These results complement that finding and describe clear frequency differences between a rural and an urban site. This study gave focus to the role that kleptoparasitism might play in helping gulls meet their energy needs when invading urban environments, however, the number of study populations compared is small – one rural and one urban environment only – and so it is necessary to be cautious when generalizing any findings. However, here I consider the mechanism by which urban invasion might occur when birds initially encounter those spaces. As Marzluff, Bowman and Donnelly (2001) have described, the foraging environment changes on a gradient between wilderness environments and heavily urbanised spaces. As a gull moves along this gradient it will encounter fewer aspects of the foraging environment with which it is familiar. At one extreme of this gradient are heavily urbanised spaces containing lots of anthropogenic novelty with few of the characteristics of a natural food web. Billingsgate is such a site, as all the food there is waste provisioned by human activities. A gull, or small founder population of gulls, invading an urban environment must either obtain food through: innovation by exploring the novel foraging space; learning what things are edible and where to find them by copying other foragers; or stealing food from other individuals.

Previous research has emphasised the importance of innovative behaviour in species that invade novel environments (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Bacher, Reader, & Lefebvre, 2008). Some proportion of innovators, who explore the environment, are essential in any population otherwise there would be no one to copy, however, rates of innovation in any natural population are quite low (Page 2008), making the second two options, copying or stealing, more likely for invasive gulls. Of these, copying other foragers to learn the locations of food is necessary but stealing can be efficient as it avoids the cost of the full foraging cycle by acquiring food discovered by another's effort. To this end, we can think of stealing information and stealing food as on a continuum; the cost of stealing the food is actually the marginal cost of stealing conditional on already observing the victim.

As gulls can range over large areas they can occupy different habitats on the gradient described above in a single foraging bout or day. This suggests a plausible alternative mechanism to the one described above by which gulls can invade urban spaces. They can forage in environments where they encounter conditions with which they are familiar, and then make forays and encroachments into urban spaces in search of supplemental food and other foraging populations. Foraging in the littoral zone of rivers and estuaries that pass near or through cities is an example of

how this might work. In arguing for the utility of kleptoparasitism I have made the assumption that while this second mechanism would undoubtedly occur, the additional travel and foraging costs involved would make it energetically more expensive than exploiting other foragers through kleptoparasitism. These costs would not be prohibitive of this foraging approach but I suggest that these additional costs would make it secondary to the kleptoparasitic strategies considered above. At present little is known about the foraging habits and ranges of urban gull populations, and tracking of individuals to see the extent of their foraging ranges was not undertaken in this study. Further work of this nature would be useful to assess whether urban gull populations, such as the one at Billingsgate, obtain their food exclusively at that site or exploit a variety of habitats.

Comparing the range and diversity of environments occupied by different gull species may also provide insights into the role of kleptoparasitism in supporting invasion. As described by Brockmann & Barnard (1979) 23 of 88 gull species are reported to use kleptoparasitism (See Chapter 2, Table 1.1). A comparison between kleptoparasitic and non-kleptoparasitic gull species of the diversity of habitats that these species routinely breed and forage in, and the extent of their ranges, may provide indirect evidence for the proposed role of kleptoparasitism as a strategy that buffers against environmental change. If this proposed function of kleptoparasitism is plausible we should expect to see kleptoparasitic gull species occupying a broader diversity of habitats than non-kleptoparasitic gull species.

4.5.2 – Ecological predictors of kleptoparasitism

Birds are dispersed widely at Brancaster and population density was positively correlated with kleptoparasitism. This finding is consistent with empirical research that shows foragers are more likely to encounter each other at high population densities and interact aggressively (Colwell 2010). It also lends support to the theoretical model of Hamilton (2002) demonstrating increased kleptoparasitism with increasing competitor density.

In addition, King, Isaac and Cowlishaw (2009), in research on baboon troops, found that the distribution of resources influenced the rate of kleptoparasitism, with small tightly clustered patches prompting more kleptoparasitism (See chapter 2 section 2.3.4). The resources in the study environments at Brancaster and Billingsgate were clearly distributed in different ways that provided a useful test of the pattern of behaviour described by King et al. (2009). The food at Brancaster was naturally more widely dispersed throughout the environment and it was a much larger study area than Billingsgate, permitting gulls to be more spaced out whilst foraging. The results of the current study support the finding of King et al. (2009) with more kleptoparasitism in high density areas where gulls were forced to forage closer together, perhaps making it easier to take advantage of opportunities to try and steal.

The finding that larger food items were more likely to be targeted for theft is in accord with the findings of several empirical studies (Hopkins & Wiley 1972, Ens & Cayford 1996, Leeman, Colwell, Leeman, & Mathis, 2001). Large prey items provide a conspicuous visual cue to the presence of food, and a large prey item requires longer handling time, which increases the likelihood that other foragers

can approach and try to steal the item. My use of an ordinal scale to measure the size of prey items in terms of bill lengths was a limitation of this study that may have resulted in a loss of additional data of value. Ordinal measures of this kind result in a lack of precision that may mask useful patterns of behaviour. A more finely grained measure would have been beneficial, but the ordinal measure of bill lengths used represented the most practical way to assess the size of food items from the observational data obtained.

The slightly negative correlation between prey size and kleptoparasitism rate seen at Brancaster is likely a reflection of the overall predominance of smaller sized prey items at that site and a lack of larger prey items above a certain size. As nearly all food items at Brancaster were very small and decreased in abundance with increasing size it is unsurprising that any kleptoparasitic attempt observed was likely to feature a contest over a small item of food.

4.6 – Summary

In this chapter I have outlined the analyses and results of study 1. The results showed that kleptoparasitism in gulls occurred at a greater rate at an urban compared with a coastal site and that population density and prey size predicted the rate of kleptoparasitism at the urban site. These results suggest that kleptoparasitism may well aid invasion and increase the range of environments a gull can tolerate by helping them meet their energy needs in novel environments where normal foraging behaviours are difficult to implement.

In the next chapter I go on to discuss the analyses and results of study 2. Having established a difference in the rate of kleptoparasitism between the two study environments in this study, in study 2 I look at each study site in more detail to examine the patterns of kleptoparasitic behaviour that were seen at those locations.

* *The research reported in this chapter was published in the peer-reviewed journal Bird Study in November 2016. A copy of the draft manuscript for this paper is attached as Appendix M.*
The reference for the article is: Spencer, R., Russel, Y.I., Dickins, B.J.A. & Dickins, T.E. (2016). Kleptoparasitism in gulls Laridae at an urban and a coastal foraging environment: an assessment of ecological predictors, *Bird Study*, DOI: 10.1080/00063657.2016.1249821

(5)

Chapter 5 – Study 2: Who commits kleptoparasitism, how, and against whom?

5.1 – Introduction

In the previous chapter I outlined and discussed the results of study 1 which looked at differences in the overall rate of kleptoparasitism between the two study sites and assessed the ecological variables that best predicted those differences. In this chapter I look within those two study environments to describe which individuals in the populations at Brancaster and Billingsgate commit kleptoparasitism, which kleptoparasitic strategies they use, and which individuals they use those strategies against. I also assess which species were the victims (hosts) of kleptoparasitism. In addition to describing these patterns I analyse the relationship between kleptoparasitism and the extent to which species and age-classes associate whilst foraging, as well as considering differences in the extent to which different species age-classes were kleptoparasites and hosts.

5.2 – Study rationale and predictions

This study addressed the second research aim of this thesis (Chapter 2, section 2.4) by investigating the behaviour seen in competitively asymmetric foraging populations. I describe and interpret the main patterns of kleptoparasitic behaviour recorded at the two study sites to understand how kleptoparasitic behaviours are used in mixed-species foraging aggregations of gulls. The following analyses were used to address the second research aim (Chapter 2, Table 2.1 and section 2.4).

Is there a species and age difference in the use of kleptoparasitism? Gull species differ in size and strength, and foraging ability in gulls increases with age up to maturity at between 2 and 4 years depending on species (Verbeek, 1977a). These are key dimensions on which individuals in mixed-species gull populations differ in terms of competitive ability. Theoretical models have suggested that less efficient foragers should engage in more kleptoparasitic behaviours and also that dominant individuals should make more use of kleptoparasitism (Hamilton, 2002; Holmgren, 1995). In gull populations this would mean both subordinate and dominant individuals exploiting kleptoparasitic opportunities to some degree and suggests complex patterns of kleptoparasitism use may be seen in mixed-species gull populations. In line with this prediction, both larger gull species and juvenile gulls should commit more kleptoparasitism. In order to describe and understand the patterns of behaviour in the study populations used for this thesis an analysis was conducted of the way species and age-classes are distributed in relation to kleptoparasitic incidents. This analysis addressed key question 3 outlined for research aim 2 (Table 2.1) by examining the ways in which competitive differences influence behaviour in relation to kleptoparasitism.

Which species and competitive abilities use which types of kleptoparsitism? Individuals of differing competitive abilities might use different kleptoparasitic strategies to compete for resources. Little research has been conducted to investigate the patterns of behaviour that will be seen when foragers have the ability to utilise all three types of kleptoparasitic strategy (aggressive, stealth, scramble). An examining the use of these three strategies allowed an investigation of the value of kleptoparasitism as a flexible foraging strategy and showed which species used which strategies against different opponents.

Investigating how kleptoparasitism strategies were used by different levels of competitor in the population also permitted an assessment of whether the use of stealth kleptoparasitism provided an empirical validation of the Marauder (strategy X) foraging type described by Broom, Luther, Ruxton and Rychtar (2008) and Maynard Smith (1982). This was achieved by assessing whether stealth kleptoparasitism was a strategy used by subordinate foragers against dominant individuals to obtain food items, which they would subsequently relinquish without a fight if challenged. These analyses addressed key questions 4 and 5 of research aim 2 (Table 2.1) by examining how the ability to use different types of kleptoparasitism influences the patterns of behaviour observed, and whether stealth kleptoparasitism is an example of a Marauder strategy used by subordinate individuals.

What level of success do the different species and competitors have when using the three types of kleptoparasitic strategy? The use of a type of kleptoparasitic strategy should be correlated with its success rate and payoff. Kleptoparasitism is a foraging strategy used flexibly by gulls, as such we should expect them to make good decisions and invest more in effective kleptoparasitic strategies and less in ineffective strategies. The effective or, vice versa, ineffective but persistent use of a strategy will help us to understand the adaptive-value of kleptoparasitism for gulls and also the behavioural flexibility of gulls. If gulls used the three kleptoparasitic behaviours adaptively, then we should expect to see the use of a type of kleptoaprasitism being influenced by its success rate as a function of the competitive ability of the opponent. This analysis gave further consideration to key question 4 outlined for research aim 2 (Table 2.1) regarding the influence of different types of kleptoparasitism on the behaviour of foragers.

Predictions: A number of predictions were made in relation to the three analyses outlined above. First, at the coastal site (Brancaster) it was predicted that kleptoparasitism would be correlated with the strength of association between species. This was predicted because the study site was a large beach area; this expanse of foraging space was expected to permit gulls to separate into foraging groups that better reflected competitive ability. For example, smaller gull species may be able to avoid foraging alongside larger, more dominant, gull species by occupying or moving to different parts of the beach. Such segregation will be reflected in the kleptoparasitic interactions of these species, with those aggregating together at a higher rate committing more kleptoparasitism against one-another.

Second, in line with the predictions of Hamilton (2002) and Holmgren (1995), it was predicted that across the sites juvenile birds would compensate for their lower foraging ability by committing a disproportionate amount of kleptoparasitism relative to their presence in the population. In addition,

the lower foraging skill of juvenile gulls was also expected to make them potentially easier targets for kleptoparasites, so it was predicted they would be hosts to a disproportionate amount of kleptoparasitic incidents.

Third, the prediction was made that the use of different types of kleptoparasitism would reflect an assessment of the competitive differences between the parasite and host, and the likely costs and probability of success. It was predicted that subordinate birds would use stealth against more dominant individuals as their competitive inferiority would exclude them from using aggressive kleptoparasitism. It was also predicted that these subordinate users of stealth kleptoparasitism would not defend the food items if they were handling the item and were subsequently attacked by a more dominant kleptoparasite. If correct this prediction would provide an empirical demonstration of the existence of a Marauder strategy (strategy X).

The final prediction made for this study was that there would be little scramble kleptoparasitism committed (Chapter 3, section 3.4.2). Although gulls are gregarious, their sociality is not significantly complex and the coefficient of relatedness (Hamilton, 1964) between individuals within foraging flocks is predicted to be low. As stated previously (Chapter 1, section 1.4), they do not remain in kin-bonded groups after fledging, and their sociality largely involves competitive interactions around food. This suggests that gulls may lack the social cognition to coordinate their behaviour in a manner that would permit the effective use of scramble kleptoparasitism, especially when food sources are not easily divisible.

5.3 – Analyses

The field data on population sizes and composition (Chapter 3, section 3.4.1) and the types of kleptoparasitic strategy observed (Chapter 3, sections 3.4.2.1, 3.4.2.2 and 3.4.2.3) were used in this study. In the following sections I describe how those data were treated in order to conduct the various analyses of interest.

5.3.2 – Population composition: The composition of the populations at Brancaster and Billingsgate were calculated using two methods. The first used headcount photos to count the total size and composition of the populations present at both sites (Chapter 3, sections 3.4.1, 3.5.1 and 3.5.2). The second used headcounts at foraging patches, obtained from foraging patch videos, to calculate the number and composition of gull species engaged in foraging behaviour. Videos of foraging patches were watched and a record made of the species and ages of all individuals that attended the patch to forage. Using headcounts from photos capturing the total population, and headcounts from patch videos permitted a comparison to be made of whether the proportions of each species engaged in foraging differed greatly from the proportions of each species in the population as a whole. Population comparisons for both study sites showed a great deal of correspondence between the composition of the total population and the composition of foraging patches, as can be seen in Table 5.1.

The focus of this second study was an investigation within the study populations of the patterns of kleptoparasitic behaviour. As that behaviour occurred within foraging patches, the composition data on species and age-classes obtained from patches were used for all analyses.

Table 5.1. Species composition of populations at Brancaster and Billingsgate calculated using headcounts at patches, and total population headcounts. Values for each species give percentage of population. The study species were Black-headed gull (BHG), Herring gull (HG), Great Black-backed gull (GBB) and Common gull (CG).

Site	Method	BHG	HG	GBB	CG
Brancaster	Population	36	42	3	19
	Patch	37	35	2	26
Billingsgate	Population	19	70	11	-
	Patch	16	72	12	-

5.3.3 – Kleptoparasitism data: Foraging videos recorded at the two study sites were viewed and kleptoparasitic events were recorded as frequency counts. Several details were recorded for each kleptoparasitic incident, these included the species and age of the kleptoparasite, the species and age of the host, the type of kleptoparasitic strategy used (Chapter 3, section 3.4.2), and whether the attempt was successful or not. In addition, details of whether a host attempted to defend its food item or immediately surrendered it were recorded where it was possible to ascertain that host's response.

The data on kleptoparasitism was analysed to obtain details of kleptoparasitic interactions, strategies, and success rates, at the species level, at the age-class level (Chapter 3 section 3.4.1) generalised for the whole population, and also by discriminating each species by age-class. The host response data (defend or surrender) was analysed at the species level as this was main level of asymmetry in resource holding potential (RHP – Chapter 2, section 2.4) identified through size differences between species. Analyses were conducted for the two study sites separately to obtain an understanding of the main patterns of kleptoparasitism within those environments.

5.3.4 – Strength of association: The strength of association between different species whilst foraging was obtained by counting the frequency with which each study species appeared together at patches. The percentage of foraging patches in common between species was calculated, and was used as a measure of the extent to which those species associated whilst foraging, this included single species patches containing multiple conspecifics. Similarly, the frequency of patches in common between different age-classes was used to calculate the strength of association whilst foraging between age-classes as a percentage figure, including patches containing multiple individuals from just one age-class. These strength of association percentages were correlated with kleptoparasitism counts to show the extent to which the species or ages kleptoparasitized each other, expressed as a percentage of the total kleptoparasitism committed by each species or age-class. The data for Billingsgate and Brancaster was analysed separately, and was tested to see if assumptions of normality and homogeneity of variance were met. Shapiro-Wilk test was used to assess whether the

data for each site was normally distributed, and Hartley's F_{max} was used to test for homogeneity of variance. A correlation analysis was then conducted between the percentage of kleptoparasitism and the strength of foraging association between species or age-classes. Dependent on the result of the tests of normality and homogeneity of variance, either parametric or non-parametric correlational tests were used for the different analyses.

5.3.5 – Kleptoparasite and host comparison by species age-class: The most fine-grained categorisation that could be made of the study species was to distinguish each species by age-class. These *species age-classes* were used to assess whether there was a significant difference in the rate at which individuals in a species age-class committed kleptoparasitism, and the rate at which they were the hosts to kleptoparasites. Each species age-class composed different proportions of the total foraging population, these differences should have an influence on the rate at which the species age-class committed or experienced kleptoparasitism. To control for these differences a weighted kleptoparasitism and host score was obtained for each species age-class by dividing the percentage of occasions a species committed or was host to kleptoparasitism by the percentage of the population composed by that species age-class, as shown in equations (1) and (2).

$$Weighted\ kleptoparasitism\ score = \frac{\%\ kleptoparasitism\ committed}{\%\ of\ population} \quad (1)$$

$$Weighted\ host\ score = \frac{\%\ occasions\ host}{\%\ of\ population} \quad (2)$$

As each species age-class had only two weighted scores, one for kleptoparasitism committed and one for kleptoparasitism experienced, it was not possible to conduct meaningful inferential statistical analyses on the data to see which species age-classes differed in the extent to which they were kleptoparasites and hosts. Consideration was given to conducting a Chi square analysis on the unweighted scores, however, multiple violations of the expected frequencies for cells meant no valid analysis could be carried out. To investigate whether there was a contrast for any species age-class in amount of kleptoparasitism they committed, and the number of occasions they were hosts, bar charts were used to make a visual comparison of the scores for the two categories.

5.3.6 – Kleptoparasitism by Dominant and Subordinate foragers: Further analyses were conducted to try and confirm the patterns described in the data regarding kleptoparasitic behaviours at both Billingsgate and Brancaster. For these analyses individuals in the study populations were dichotomised into two status categories as either *dominant* or *subordinate* using two criteria: size and foraging ability. Size is a clear indicator of differences in strength between gulls, it is an asymmetry that is readily perceived and will therefore influence the outcome of contests between individuals (Maynard Smith, 1982). Foraging ability is something that has been shown to improve in gulls with age and experience up to maturity (Verbeek, 1977a; Bertelotti & Yorio, 2000). The dominant category

consisted of all 3 age-classes (adult, sub-adult, juvenile) of Great Black-backed gulls (GBB: *Larus marinus*) and adult Herring gulls (HG: *Larus argentatus*). The subordinate category contained sub-adult and juvenile HG, all age-classes (adult, sub-adult, juvenile) of Common gull (CG: *Larus canus*) and both age-classes (adult, juvenile) of Black-headed gulls (BHG: *Chroicocephalus ridibundus*). All age-classes of GBB were considered dominant because of their large size and aggression, even when juveniles, and all age-classes of CG and BHG were considered subordinate because of their smaller size. Using these criteria to divide the known population composition at Billingsgate, the dominant category made up 40% and the subordinate category made up 60% of the population. At Brancaster the dominant category made up 27.5% of the population and the subordinate group 72.5%. Chi-square analyses were used to investigate differences between the dominant and subordinate categories on the use of aggressive and stealth kleptoparasitism and on success and failure when using kleptoparasitism.

5.4 – Results

5.4.1 – Billingsgate:

5.4.1.1 – Population composition at Billingsgate: The composition of the population of foraging gulls at Billingsgate by species and age is shown in Table 5.2. A large majority of the population were HG (72%), of which juvenile birds were by far the largest group making up 39% of the total foraging population. This age difference was true of GBB also, which as a species accounted for 12% of the foraging population, with the majority of those GBB being juvenile birds (8%). The opposite pattern with respect to age was seen with BHG. BHG constituted 16 % of the foraging population, the vast majority of these were adult birds, with juvenile BHG making up only 1% of the total population. This preponderance of adults amongst the BHG was likely a result of the two-year moult to adult plumage seen in this species; meaning, there is no discernible sub-adult plumage category that can be easily identified from field observations. In order for a BHG to be categorised as juvenile using this method they had to be well within the first year of life, before the first complete summer moult. In contrast the larger gulls can still retain the brown plumage typical of a juvenile well into the second winter giving a longer period in which they can be safely classified as juvenile birds.

Table 5.2. Billingsgate population composition by species and age. Values represent the percentage proportion of the total foraging population.

Species	BHG	HG	GBB
Population %	16	72	12
Age %			
Adult	15	19	2
Sub-adult	-	14	2
Juvenile	1	39	8

5.4.1.2 – Kleptoparasitism at Billingsgate: In total 595 kleptoparasitic events were recorded at Billingsgate over the year of study. Table 5.3 shows the frequencies of these kleptoparasitic incidents discriminated at the level of the species, age and kleptoparasitic strategy used. Tables 5.4 and 5.5 provide summaries of the main patterns of behaviour that can be discerned from the results shown in Table 5.3. Table 5.4 shows the kleptoparasitism committed by each species, and Table 5.5 shows the occasions when each species was the host being kleptoparasitized. Table 5.6 shows the frequencies with which hosts defended and surrender food items against kleptoparasitic attacks at the species level. I will interpret and describe the main patterns of behaviour shown in these tables in the discussion section later in this chapter (section 5.5.1).

Table 5.3. Kleptoparasitic interactions at Billingsgate. Kleptoparasite and host are shown by species, age, and kleptoparasitic strategy used. Values are frequency counts of kleptoparasitism incidents and the frequency of those incidents that were successful is shown in brackets.

Kleptoparasite: Species & Age	Host: Species & Age / Strategy	GBB Adult	GBB Sub-adult	GBB Juvenile	HG Adult	HG Sub-adult	HG Juvenile	BHG Adult	BHG Juvenile
GBB Adult	Aggressive	1 [1]	4 [4]	14 [13]	6 [5]	0	11 [10]	0	0
	Stealth	1 [0]	0	1 [1]	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0
GBB Sub-adult	Aggressive	0	1 [1]	5 [3]	2 [1]	4 [4]	8 [7]	0	0
	Stealth	0	0	4 [2]	0	0	2 [2]	0	0
	Scramble	0	0	0	0	0	0	0	0
GBB Juvenile	Aggressive	3 [2]	8 [6]	40 [33]	9 [9]	9 [9]	42 [39]	1 [1]	0
	Stealth	3 [3]	1 [1]	8 [6]	0	0	1 [1]	0	0
	Scramble	0	0	0	0	0	0	0	0
HG Adult	Aggressive	0	0	1 [0]	14 [10]	1 [1]	14 [12]	4 [4]	0
	Stealth	5 [2]	1 [1]	3 [2]	1 [1]	0	2 [2]	0	0
	Scramble	0	0	0	2 [1]	0	0	0	0
HG Sub-adult	Aggressive	0	0	1 [0]	3 [2]	3 [3]	8 [3]	1 [1]	0
	Stealth	3 [2]	2 [1]	9 [7]	4 [2]	1 [0]	1 [1]	0	0
	Scramble	0	1 [1]	0	1 [1]	0	1 [0]	0	0
HG Juvenile	Aggressive	4 [0]	1 [1]	3 [0]	14 [8]	8 [6]	88 [63]	11 [11]	1 [1]
	Stealth	23 [13]	2 [2]	78 [60]	16 [11]	3 [2]	26 [15]	0	0
	Scramble	0	2 [1]	0	9 [8]	0	2 [0]	0	0
BHG Adult	Aggressive	0	0	0	0	0	0	9 [9]	2 [1]
	Stealth	2 [1]	0	6 [6]	0	0	1 [1]	4 [4]	0
	Scramble	0	0	0	0	0	0	0	0
BHG Juvenile	Aggressive	0	0	0	0	0	0	2 [1]	1 [1]
	Stealth	0	0	0	0	0	0	0	1 [0]
	Scramble	0	0	0	0	0	0	0	0

Table 5.4. Summary of kleptoparasitic behaviours committed by Billingsgate gulls differentiated by species, age, type, and level of success experienced by kleptoparasites.
Success categories show the percentage of occasions that species or species age-class successfully used the different types of kleptoparasitic strategy to steal food items.

Species	Kleptoparasitism %	Age	Kleptoparasitism %	Type	Kleptoparasitism %	Success %	Success by age %
GBB	31	Adult	6	Aggressive	6	92	89
				Stealth	0.33	50	
				Scramble	0		
		Sub-adult	4	Aggressive	3	80	77
				Stealth	1	67	
				Scramble	0		
		Juvenile	21	Aggressive	19	88	88
				Stealth	2	85	
				Scramble	0		
HG	64	Adult	8	Aggressive	6	79	75
				Stealth	2	67	
				Scramble	0.34	50	
		Sub-adult	7	Aggressive	3	56	62
				Stealth	3	65	
				Scramble	0.5	67	
		Juvenile	49	Aggressive	22	69	69
				Stealth	25	69	
				Scramble	2	69	
BHG	5	Adult	4	Aggressive	2	91	92
				Stealth	2	92	
				Scramble	0		
		Juvenile	1	Aggressive	0.5	67	50
				Stealth	0.33	0	
				Scramble	0		

Table 5.5. Summary of Billingsgate host data showing hosts (victims) of kleptoparasitic attempts by species, age, type and percentage of time they were successfully parasitized.

Species	Host %	Age	Host %	Type	Host %	Success %
GBB	41	Adult	7	Aggressive	1.3	37.5
				Stealth	6.2	57
				Scramble	0	
		Sub-adult	4	Aggressive	2.3	86
				Stealth	1	83
				Scramble	0.5	67
		Juvenile	29	Aggressive	10.8	76.5
				Stealth	18	77
				Scramble	0	
HG	53	Adult	14	Aggressive	8	73
				Stealth	3.5	66
				Scramble	2	83
		Sub-adult	5	Aggressive	4	92
				Stealth	0.7	50
				Scramble	0	
		Juvenile	35	Aggressive	29	78
				Stealth	5	66
				Scramble	0.5	0
BHG	6	Adult	5	Aggressive	5	96
				Stealth	1	100
				Scramble	0	
		Juvenile	1	Aggressive	1	75
				Stealth	0.2	0
				Scramble	0	

Table 5.6. Frequency with which hosts defended and surrendered food items against kleptoparasitic attacks. Data for interactions between kleptoparasites and hosts is shown at the species level as species differences represent the main competitive asymmetry in the study populations. Defend or surrender behaviours were attributed to hosts for 330 of the 595 kleptoparasitic incidents recorded at Billingsgate (N=330).

Host	GBB		HG		BHG	
Kleptoparasite	Defend	Surrender	Defend	Surrender	Defend	Surrender
GBB	25	37	1	44	0	1
HG	33	27	76	62	0	7
BHG	0	6	1	0	2	8

5.4.1.3 - Strength of association:

Species: The data showing the strength of association between species and the extent to which those species kleptoparasitized each other at Billingsgate is shown in Table 5.7.

Table 5.7. Strength of association between species at Billingsgate and kleptoparasitism rate between those species. Strength of association is represented as percentage of patches in common between individuals of the species composing the patch, and kleptoparasitism is expressed as a percentage of the total kleptoparasitism committed by those species against individuals of the species that composed the patch.

Patch Composition (Species)	Strength of Association	Kleptoparasitism
BHG	68	67
HG	93	59
GBB	50	49.75
GBB & HG	54	41
GBB & BHG	38	4
HG & BHG	61	4

Shapiro-Wilk test of normality on the strength of association data and kleptoparasitism data shown in Table 5.7 indicated that the data was normally distributed (Strength of association: W=0.95, p=0.75; Kleptoparasitism: W=0.86, p=0.19); and analysis using Hartley's F_{max} returned an F-ratio indicating that the variances of the two categories were homogenous (F*=2.11 < 7.15). As a result Pearson's correlation test was conducted on the data, this showed there was no correlation between the strength of association between species and the extent to which those species kleptoparasitized each other, r=0.59, p=0.11, whilst foraging at Billingsgate.

Age-class: Table 5.8 shows the data for strength of association between age-classes at Billingsgate and the extent to which birds of those ages kleptoparasitized each other.

Table 5.8. Strength of association between age-classes at Billingsgate and kleptoparasitism rate between those age-classes. Strength of association is represented as percentage of patches in common between individuals of those age-classes, and kleptoparasitism is expressed as a percentage of total kleptoparasitism committed by those age-classes against individuals of age-classes composing the patch.

Patch Composition (Age)	Strength of Association	Kleptoparasitism
Adult	91	22
Sub-adult	64	11
Juvenile	96	57
Adult & Sub-Adult	60	7
Adult & Juvenile	87	28
Sub-adult & Juvenile	64	15

The data in Table 5.8 was tested for normality and homogeneity of variance. Shapiro-Wilk test indicated that the data for both categories was normally distributed (Strength of association: W=0.84,

p=0.12; Kleptoparasitism: W=0.86, p=0.18). Hartley's F_{max} test indicated that the variances for the two groups were homogenous (F*=1.28 < 7.15). A correlation analysis was conducted using Pearson's correlation coefficient; this showed there was a significant positive correlation between the strength of association between age-classes and the extent to which individuals in those age-classes kleptoparasitized each other, r=0.84, p=0.02, whilst foraging at Billingsgate.

5.4.1.4 - *Kleptoparasite and host comparison by species age-class:*

Scores, weighted to account for population composition, for the amount of kleptoparasitism committed by each species age-class, and the number of occasions each species age-class was host to kleptoparasitic attempts are shown in Table 5.9.

Table 5.9. Weighted kleptoparasitism and host scores for each species age-class at Billingsgate. Weighted scores were obtained by dividing the percentage of kleptoparasitism committed or hosted by each species age-class by the percentage of the foraging population that species age-class composed, following equations shown in section 5.3.5.

Species age-class	Kleptoparasitism Score	Host Score
GBB Adult	3	3.5
GBB Sub-adult	2	2
GBB Juvenile	2.63	3.63
HG Adult	0.42	0.74
HG Sub-adult	0.5	0.36
HG Juvenile	1.26	0.9
BHG Adult	0.26	0.33
BHG Juvenile	1	1

To investigate which species age-classes showed a difference in the rate at which individuals in that category committed kleptoparasitism and the rate at which they were the hosts of attacks by kleptoparasites, the data shown above in Table 5.9 was examined visually using the bar chart shown in Figure 5.1.

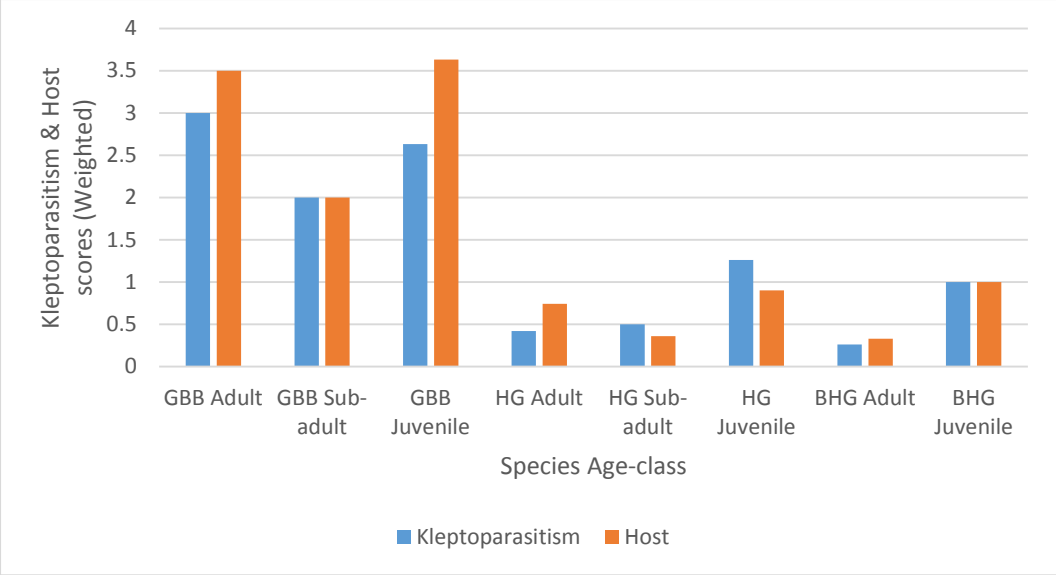


Figure 5.1. Bar chart showing a comparison of the rate at which each species age-class committed and was the host to kleptoparasitism at Billingsgate. The data for both kleptoparasitism and host rate depicts scores weighted to account for differences in the number of each species age-class in the foraging population.

Figure 5.1 shows that when the percentage of the foraging population made-up by a species age-class is controlled for GBB of all three age-classes were involved in a larger proportion of kleptoparasitic interactions as both parasite and host. However, Figure 5.1 appears to indicate that adult and juvenile GBB were the hosts to kleptoparasitism at a higher rate than they actually committed kleptoparasitism. Amongst the HG age-classes juveniles were involved in more kleptoparasitic interactions than the other two age-classes, and actually made greater use of kleptoparasitism than the rate at which they were the hosts to kleptoparasitic attempts. However, the rate at which they were hosts was still higher than the other two HG age-classes. Sub-adult HG committed kleptoparasitism at a higher rate than the rate at which they were hosts, but a visual inspection of Figure 5.1 does not suggest these two rates differed significantly. The rate at which adult HG were kleptoparasites and hosts did differ, with adult HG being hosts to kleptoparasitic attempts more often than the number of occasions they acted as kleptoparasites. BHG juveniles were engaged in kleptoparasitic interactions, as both parasite and host, at a higher rate than adult BHG when the proportions of these age-classes in the foraging population was controlled for. However, the extent to which both juvenile and adult BHG were parasites and hosts did not differ significantly.

5.4.1.5 – Kleptoparasitism by Dominant and Subordinate foragers: Table 5.10 shows the frequency with which gulls in the two status groups (dominant/ subordinate, section 5.3.6) were successful or failed in their kleptoparasitic attempts. A Chi-square analysis showed there was a significant association between the success rate of a bird and its status, $X^2(1) = 16.39$, $p<0.001$. Cramer's V was 0.17 indicating about 3% of the variation in the frequency of success and failure was explained by the status group of the birds. Examination of standardized residuals showed that in the dominant group

significantly more birds were successful (z = 1.6) and significantly fewer failed (z = -2.7) in their kleptoparasitic attempts, these results were significant at the p<0.05 level. Within the subordinate group standardized residuals showed that fewer birds than expected were successful (z = -1.3) and significantly more birds failed (z = 2.2) in their kleptoparasitic attempts, these values were also significant at p<0.05. These results support the idea that dominant individuals were more likely to be successful than subordinates in their use of kleptoparasitism at Billingsgate.

Table 5.10. Contingency table showing the frequency scores for success and failure in their use of kleptoparasitic strategies for status categories at Billingsgate.

	Success	**Failure**
Dominant	200	37
Subordinate	250	108

Table 5.11 shows the data for the second analysis relating to status at Billingsgate, this was the frequencies with which dominant and subordinate birds used aggressive and stealth kleptoparasitic strategies. A Chi-square analysis showed there was a significant association between the type of kleptoparasitic strategy used and the status of the bird $X^2(1) = 91.44$, p<0.001. Examination of Cramer's V (0.40) indicated that about 16% of the variation in the type of kleptoparasitic strategy used could be explained by the status group of the birds. Standardized residuals showed that in the dominant group significantly more birds were likely to use aggressive kleptoparasitism (z = 4.5) and significantly fewer used stealth kleptoparasitism (z = -5.8), both of these results were significant (p<0.05). Standardized residuals for the subordinate status category showed significantly less use of aggressive kleptoparasitism (z = -3.7) and significantly more subordinate birds using stealth kleptoparasitism (z = 4.8). Again, both of these values were significant at the p<0.05 level. The conclusion drawn from analysing the type of kleptoparasitism used in relation to these broad status categories confirmed what was observed at the species level, that subordinate gulls made greater use of stealth kleptoparasitism at Billingsgate.

Table 5.11. Contingency table showing the frequency scores with which aggressive and stealth kleptoparasitic strategies were used by dominant and subordinate gulls at Billingsgate.

	Aggressive	**Stealth**
Dominant	202	33
Subordinate	160	182

5.4.2 – Brancaster:

5.4.2.1 – Population composition at Brancaster: The composition of the population of foraging gulls at Brancaster by species and age is shown in Table 5.12. The largest species group in the population were the BHG who made up 36.5% of the total foraging population. This was followed by HG making up 35%, and Common gulls (CG: *Larus canus*) who composed 26% of the population. These figures show that, on the whole, the foraging population was relatively evenly spread between these three species, with no single species being predominant in the environment. In contrast, GBB made up only a very small percentage (2.5%) of the total foraging population. Across all species the majority of birds at Brancaster were adult birds, with 88% of all foraging gulls being adult birds. Sub-adult birds made up only 2.3% of the population, and juveniles only 9.2%. The majority of juvenile birds were juvenile HG, who made up 8% of the total population. For the other three study species, the small number of juvenile GBB probably reflects the low numbers of GBB within the total population, and the low numbers of non-adult BHG and CG is likely the result of a two year moult to adult plumage in both these species, resulting in a lack of a sub-adult age class that can be discerned in the field, a similar argument was made in relation to BHG age-classes at Billingsgate (section 5.4.1.1).

Table 5.12. Brancaster population composition by species and age. Values represent % proportion of the total foraging population.

Species	BHG	HG	GBB	CG
Population %	36.5	35	2.5	26
Age %				
Adult	36	25	2	25.5
Sub-adult	-	2	0.3	-
Juvenile	0.5	8	0.2	0.5

5.4.2.2 – Kleptoparasitism at Brancaster: Over the course of the study period 100 kleptoparasitic incidents in total were recorded at Brancaster. Two incidents were removed from the final dataset that was analysed as the outcome of these attempts was unknown. These two incidents resulted in aerial pursuits which were lost from sight before the attempt was concluded, so all analyses presented here are based on the 98 kleptoparasitic incidents for which the outcome was known. Table 5.13 shows the frequencies of these kleptoparasitic incidents discriminated at the level of the species, age and kleptoparasitic strategy used. Tables 5.14 and 5.15 provide summaries of the main patterns of behaviour that can be discerned from the results shown in Table 5.13. Table 5.14 shows the kleptoparasitism committed by each species, and Table 5.15 shows the occasions when each species was the host being kleptoparasitized. Table 5.16 shows the frequency with which hosts defended or surrendered food items against kleptoparasitic attacks at the species level. I will interpret and describe the main patterns of behaviour shown in these tables in greater detail in the discussion section 5.5.2.

Table 5.13. Kleptoparasitic interactions at Brancaster. Kleptoparasite and host are shown by species, age, and kleptoparasitic strategy used. Values are frequency counts of kleptoparasitism incidents and the frequency of those incidents that were successful is shown in brackets.

Parasite: Species & Age	Host: Species & Age / Strategy	GBB Adult	GBB Sub-adult	GBB Juvenile	HG Adult	HG Sub-adult	HG Juvenile	CG Adult	CG Juvenile	BHG Adult	BHG Juvenile
GBB Adult	Aggressive	0	0	1 [0]	2 [2]	0	2 [2]	0	0	0	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
GBB Sub-adult	Aggressive	0	0	0	0	0	0	0	0	0	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
GBB Juvenile	Aggressive	0	0	0	0	0	0	1 [1]	0	0	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
HG Adult	Aggressive	0	0	0	10 [6]	0	2 [2]	5 [4]	1 [1]	0	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
HG Sub-adult	Aggressive	0	0	0	0	0	1 [0]	0	0	0	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
HG Juvenile	Aggressive	0	0	0	8 [6]	2 [0]	6 [6]	2 [1]	1 [0]	0	0
	Stealth	0	0	0	0	0	2 [2]	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
CG Adult	Aggressive	0	0	0	1 [0]	0	0	11 [5]	0	8 [3]	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	2 [2]	0	0	0
CG Juvenile	Aggressive	0	0	0	0	0	0	1 [1]	0	0	0
	Stealth	0	0	0	0	0	1 [1]	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0
BHG Adult	Aggressive	0	0	0	0	0	0	3 [0]	0	17 [11]	0
	Stealth	0	0	0	0	0	0	0	0	4 [0]	0
	Scramble	0	0	0	0	0	0	0	0	4 [0]	0
BHG Juvenile	Aggressive	0	0	0	0	0	0	0	0	0	0
	Stealth	0	0	0	0	0	0	0	0	0	0
	Scramble	0	0	0	0	0	0	0	0	0	0

Table 5.14. Summary of kleptoparasitic behaviours committed by Brancaster gulls differentiated by species, age, type, and level of success experienced by kleptoparasites.
Success categories show the percentage of occasions that species or species age-class successfully used the different types of kleptoparasitic strategy to steal food items.

Species	Kleptoparasitism %	Age	Kleptoparasitism %	Type	Kleptoparasitism %	Success %	Success by age %
GBB	6	Adult	5	Aggressive	5	80	80
				Stealth	0		
				Scramble	0		
		Sub-adult	0	Aggressive	0		
				Stealth	0		
				Scramble	0		
		Juvenile	1	Aggressive	1	100	100
				Stealth	0		
				Scramble	0		
HG	41	Adult	18	Aggressive	18	72	72
				Stealth	0		
				Scramble	0		
		Sub-adult	1	Aggressive	1	0	
				Stealth	0		
				Scramble	0		
		Juvenile	21	Aggressive	19	68	71
				Stealth	2	100	
				Scramble	0		
CG	24	Adult	22	Aggressive	20	40	45
				Stealth	0		
				Scramble	2	100	
		Juvenile	2	Aggressive	1	100	100
				Stealth	1	100	
				Scramble	0		
BHG	29	Adult	29	Aggressive	20	55	55
				Stealth	5	0	
				Scramble	4	0	
		Juvenile	0	Aggressive	0		
				Stealth	0		
				Scramble	0		

Table 5.15. Summary of Brancaster host data showing hosts (victims) of kleptoparasitic attempts by species, age, type and percentage of time they were successfully parasitized.

Species	Host %	Age	Host %	Type	Host %	Success %
GBB	1	Adult	0	Aggressive	0	
				Stealth	0	
				Scramble	0	
		Sub-adult	0	Aggressive	0	
				Stealth	0	
				Scramble	0	
		Juvenile	1	Aggressive	1	0
				Stealth	0	
				Scramble	0	
HG	38	Adult	22	Aggressive	22	63
				Stealth	0	
				Scramble	0	
		Sub-adult	2	Aggressive	2	0
				Stealth	0	
				Scramble	0	
		Juvenile	14	Aggressive	11	91
				Stealth	3	100
				Scramble	0	
CG	28	Adult	26	Aggressive	24	57
				Stealth	0	
				Scramble	2	0
		Juvenile	2	Aggressive	2	50
				Stealth	0	
				Scramble	0	
BHG	33	Adult	33	Aggressive	25	42
				Stealth	4	0
				Scramble	4	0
		Juvenile	0	Aggressive	0	
				Stealth	0	
				Scramble	0	

Table 5.16. Frequency with which hosts defended and surrendered food items against kleptoparasitic attacks. Data for interactions between kleptoparasites and hosts is shown at the species level as species differences represent the main competitive asymmetry in the study populations. Defend or surrender behaviours were attributed to hosts for 66 of the 100 kleptoparasitic incidents recorded at Brancaster (N=66).

Host	GBB		HG		CG		BHG	
Kleptoparasite	Defend	Surrender	Defend	Surrender	Defend	Surrender	Defend	Surrender
GBB	1	0	0	4	0	0	0	0
HG	0	0	7	20	1	3	0	0
CG	0	0	0	0	3	3	4	4
BHG	0	0	0	0	1	0	11	4

5.4.2.3 - Strength of association:

Species: The data showing the strength of association between species and the extent to which those species kleptoparasitized each other at Brancaster is shown in Table 5.17.

Table 5.17. Strength of association between species at Brancaster and rate of kleptoparasitism between those species. Strength of association is represented as percentage of patches in common between individuals of the species composing the patch, and kleptoparasitism is expressed as a percentage of the total kleptoparasitism committed by those species against individuals of the species in that patch.

Patch Composition (Species)	Strength of Association	Kleptoparasitism
BHG	68	89
HG	82	78
GBB	28	16.5
CG	61	59
GBB & HG	26	9
GBB & CG	13	0.03
GBB & BHG	18	0
HG & CG	49	17
HG & BHG	51	0
CG & BHG	50	21

The data in Table 5.17 was tested for normality of distribution using the Shapiro-Wilk test. This showed that while the data for strength of association was normally distributed the kleptoparasitism data was significantly non-normally distributed (Strength of association: W=0.95, p=0.69; Kleptoparasitism: W=0.81, p=0.02). An F-ratio test was conducted using Hartley's F_{max} that showed that the variances of these two categories were likely homogenous (F*=2.2 < 4.03), however, due to the fact that the distribution of the kleptoparasitism scores was significantly non-normal a non-parametric statistical test was used. Spearman's correlation coefficient showed that the strength of association between species whilst foraging at Brancaster and the extent to which those species attempted to kleptoparasitize each other was significantly positively correlated, r_s=0.75, p=0.006.

Age-class: Table 5.18 shows the data for strength of association between age-classes at Brancaster and the extent to which individuals of those age-classes kleptoparasitized each other.

Table 5.18. Strength of association between age-classes at Brancaster and kleptoparasitism rate between those age-classes. Strength of association is represented as percentage of patches in common between individuals of those age-classes, and kleptoparasitism is expressed as a percentage of total kleptoparasitism committed by those age-classes against individuals of the age-classes composing the patch.

Patch Composition (Age)	Strength of Association	Kleptoparasitism
Adult	99	92
Sub-adult	27	0
Juvenile	51	42
Adult & Sub-Adult	27	0
Adult & Juvenile	50	19
Sub-adult & Juvenile	25	12

The strength of association data and kleptoparasitism data shown in Table 5.18 was tested for normality and homogeneity of variance. Shapiro-Wilk test showed that the kleptoparasitism data was normally distributed but the data for strength of association was significantly non-normal (Strength of association: W=0.79, p=0.05; Kleptoparasitism: W=0.83, p=0.1). Hartley's F_{max} test for homogeneity of variance indicated that the data for these two categories showed homogenous variances (F*=1.54 < 4.03). As a consequence of the significant non-normal distribution of the strength of association data, Spearman's non-parametric correlation coefficient was used. The results showed a significant positive correlation between the strength with which different age-classes associated whilst foraging and the extent of kleptoparasitism between individuals of those age-classes, r_s=0.82, p=0.02.

5.4.2.4 - *Kleptoparasite and host comparison by species age-class:*

Data for Brancaster giving scores, weighted for population composition, for kleptoparasitism committed and the percentage of time each species age-class was host to kleptoparasitic attempts is shown in Table 5.19.

Table 5.19. Weighted kleptoparasitism and host scores for each species age-class at Brancaster. Weighted scores were obtained by dividing the percentage of kleptoparasitism committed or hosted by each species age-class by the percentage of the foraging population that species age-class composed, following equations shown in section 5.3.5.

Species age-class	Kleptoparasitism Score	Host Score
GBB Adult	2.5	0
GBB Sub-adult	0	0
GBB Juvenile	5	5
HG Adult	0.72	0.84
HG Sub-adult	0.5	1
HG Juvenile	2.63	1.75
CG Adult	0.86	0.98
CG Juvenile	4	4
BHG Adult	0.81	0.92
BHG Juvenile	0	0

Figure 5.2 shows a bar chart depicting the data outlined in Table 5.19. This was examined visually to investigate whether any species-age class differed significantly in the rate at which it committed or was the host of kleptoparasitism once differences in the proportion of each species age-class in environment were controlled for.

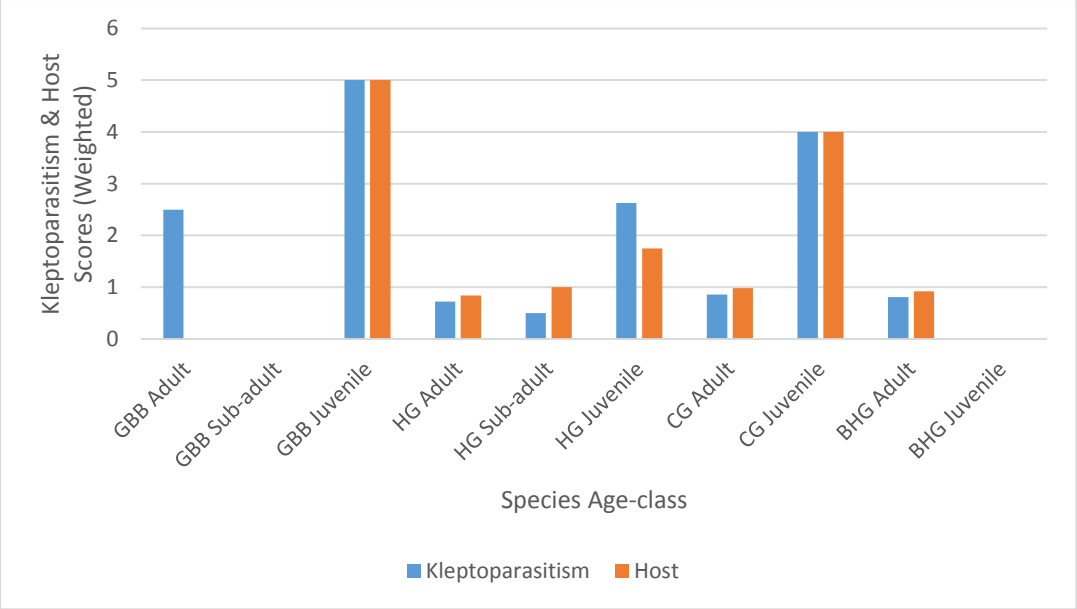


Figure 5.2. Bar chart showing a comparison of the rate at which each species age-class committed and was the host to kleptoparasitism at Brancaster. The data for both kleptoparasitism and host rate depicts scores weighted to account for differences in the number of each species age-class in the foraging population.

As is apparent in Figure 5.2 no data points were recorded for GBB sub-adult and BHG juveniles, this is likely the result of individuals from these two species age-classes only occurring at very low levels in the Brancaster study environment as opposed to recording anything concrete about the use of kleptoparasitic strategies by these two species age-classes. GBB adults committed kleptoparasitism but no observations were made of occasions when they were the hosts of kleptoparasitic attempts to steal their food. Aside from the high rate of kleptoparasitism committed by adult GBB, the most significant pattern shown in Figure 5.2 was that, excluding the BHG, juvenile birds were involved in kleptoparasitic interactions, as both kleptoparasite and host, at a much higher rate than any other age-class. This was true when looking at age-classes within-species for the GBB, HG, and CG. The rate at which juvenile GBB committed and hosted kleptoparasitism did not differ, and neither did those rates for juvenile CG. However, juvenile HG appear to have committed significantly more kleptoparasitism than they were hosts to. A further pattern of note was that sub-adult and adult HG, adult CG, and adult BHG were all hosts to more kleptoparasitic behaviour than they committed. Adults of these three species were all hosts at a higher rate but an examination of Figure 5.2 suggests that the rates for these two categories were not significantly different. The difference in rate between these categories for sub-adult HG does, however, appear to be significant. Sub-adult HG were the host to kleptoparasitic attempts to steal their food twice as often as they attempted to use kleptoparasitic strategies.

5.4.2.5 – Kleptoparasitism by Dominant and Subordinate foragers: Table 5.20 shows the frequency scores with which gulls in the two status categories (dominant/ subordinate) were successful or failed

in their kleptoparasitic attempts. A Chi-square analysis showed no significant association between the success rate of a bird, in its use of kleptoparasitism, and that bird's status $X^2(1) = 3.56$, p = 0.06.

Table 5.20. Contingency table showing the frequency scores for success and failure in their use of kleptoparasitic strategies for status categories at Brancaster.

	Success	Failure
Dominant	18	6
Subordinate	36	32

The second status analysis conducted at Brancaster examined the association between status group and type of kleptoparasitic strategy used (aggression or stealth). Table 5.21 shows the frequencies with which gulls in different status categories used aggressive and stealth kleptoparasitism. A Chi-square analysis showed no significant association between kleptoparasitism type and the status of birds at Brancaster, $X^2(1) = 2.67$, p = 0.10.

5.21. Contingency table showing the frequency scores with which aggressive and stealth kleptoparasitic strategies were used by dominant and subordinate gulls at Brancaster.

	Aggression	Stealth
Dominant	24	0
Subordinate	61	7

5.5 – Discussion

5.5.1 – Billingsgate:

5.5.1.1 – Kleptoparasitism committed by GBB at Billingsgate: GBB were responsible for 31% of the kleptoparasitism committed at Billingsgate (Table 5.4). This is much higher than might be predicted based on the proportion of the population made up by GBB (12% - Table 5.2), if the assumption were made that kleptoparasitism is an opportunistic foraging strategy that operates uniformly across gull species we might expect the level of kleptoparasitism engaged in to reflect the proportion of that species in the population. However, that is not the case here suggesting that GBB make a great deal of use of kleptoparasitism as a foraging strategy at Billingsgate.

Juvenile gulls were responsible for the majority of the kleptoparasitism committed by GBB, with 125 out of 189 incidents (67%) of total GBB kleptoparasitism being attempted by juveniles. This, however, is not disproportionate to their composition of the GBB population, which was about 66% juvenile birds. The GBB kleptoparasitism committed by adult GBB was 38 out of 189 incidents (19%), and sub-adult GBB committed 26 out of 189 incidents, about 14% of total GBB kleptoparasitism, this also closely reflected the proportions of these age-classes in the GBB population (Adult: 15%; Sub-adult: 19% - Table 5.2); suggesting that there is no difference in the level of investment in kleptoparasitism across the age-classes within this species.

No clear pattern of difference in the rate of success across age-classes was found. As can be seen from Table 5.4 adult GBB were successful in 89% of the kleptoparasitism they attempted, sub-adults in 77% of the kleptoparasitism they attempted, and juveniles were successful 88% of the time. There was apparently no real difference between adults and juvenile GBB in success in this population, and although sub-adult success was lower than these two, this may be the result of sampling bias due to the smaller amount of sub-adult GBB kleptoparasitism observed.

The majority of kleptoparasitism committed by GBB was aggressive kleptoparasitism, 168/189 incidents (89%), this appears to reflect the fact that the GBB is a large and powerful species, allowing it to effectively use force or threat in preference to other kleptoparasitic strategies when competing for resources. GBB made occasional use of stealth kleptoparasitism, this accounted for 21/189 incidents (11%), on nearly all of these occasions this was to attempt to steal from other GBB (86%). As stealth kleptoparasitism is a less risky but less profitable strategy than aggressive kleptoparasitism, its use by GBB at Billingsgate suggests it was used opportunistically when competitive differences made it the best option. The fact that it was rarely used by GBB against HG and BHG, which are smaller, less powerful species, provides further indication that its use reflected an assessment of competitive differences, as against these species aggressive kleptoparasitism by GBB is likely to be successful.

The majority of stealth kleptoparasitism by GBB were attempts by juveniles (62%). There are various potential asymmetries between individuals of different age-classes that can influence the

likely outcome of a contest, for example, adult plumage may signal dominance over juvenile birds prompting less risky strategies by subordinate individuals (Hogan-Warburg, 1966; van Rhijn, 1973). Stealth kleptoparasitism by GBB at Billingsgate may be a strategy used when needed by subordinate birds, it is less profitable as the parasite will rarely obtain the whole food item but is the kleptoparasitic strategy likely to result in some successful payoff when faced with a more dominant opponent.

The species targeted by GBB were: other GBB on 94/189 incidents (49.75%), HG on 94/189 incidents (49.75%), and BHG on only 1/189 incidents (0.5%). The lack of kleptoparasitism towards BHG probably marks a lack of shared food resources over which to compete, with the BHG taking a larger percentage of much smaller food items over which the GBB would have little interest in competing. The majority of GBB kleptoparasitism was aggressive kleptoparasitism, this accounted for 168 of the 189 kleptoparasitic events committed by GBB, or approximately 88% of GBB kleptoparasitism. This included the only attempt to steal from a BHG and 91 of the 94 incidents (97%) of kleptoparasitism directed by GBB against HG. When stealing from other GBB, aggressive kleptoparasitism was used on 76/94 occasions, about 80% of the time, and stealth kleptoparasitism on 18/94 occasions (20%). As stated above this strong bias towards the use of aggressive kleptoparasitism clearly reflects the GBB's size and dominance in foraging gull populations, its use being most clearly pronounced against smaller species, but still being predominant against conspecifics between whom interactions would be more evenly matched. The slightly increased use of stealth kleptoparasitism against some GBB conspecifics would seem to agree with this, and reflect, as described above in relation to its use by juveniles, a choice of strategy based on a within-species assessment by the parasite of its chances of success against a given host.

5.5.1.2 – Kleptoparasitism with GBB hosts at Billingsgate: The extent to which GBB were the hosts of kleptoparasitic attempts at Billingsgate is summarised in Table 5.5. As can be seen at the species level GBB were the victims of 41% of all the kleptoparasitism that occurred. This is much higher than might be predicted based on the fact that they composed only 12% of the population. GBB were hosts for a total of 241/595 incidents. In the majority of these cases, 173 out of 241 (72%), the host was a juvenile GBB. The remaining occasions when GBB were hosts the victim was an adult for 45/241 (19%) incidents, and a sub-adult on 23/241 (9%) occasions. As with the commission of kleptoparasitism by GBB, the frequency with which each age class was a host closely corresponded to the proportion of that age class in the environment. From these results it cannot be concluded that juveniles were disproportionally targeted by kleptoparasites as they are easier to steal from.

The species of kleptoparasite targeting GBB was split between other GBB 39%, HG 58%, and BHG 3%. To consider first BHG targeting GBB. This occurred very rarely, the 3% accounts for only 8/241 attempts to steal from GBB, all of which were instances of stealth kleptoparasitism. This makes sense based on the difference in size between these two species, a BHG is highly unlikely to experience any success using an aggressive strategy against GBB, so, a less risky stealth strategy, in which BHG can use their smaller size and agility, is the more plausible option for a BHG attempting to kleptoparasitize a GBB. This provides a further indication that stealth kleptoparasitism is a strategy

likely to be utilised by subordinate individuals when competing for resources, as mentioned in section 5.5.1.1.

HG were the biggest parasites of GBB, accounting for the 139/241 attacks on GBB. However, the type of kleptoparasitism used by HG in these interactions likely reflects the competitive differences between these species. Aggressive kleptoparasitism was attempted on only 10/139 or 7% of occasions, and some scramble kleptoparasitism was attempted by HG on GBB but this was very rare accounting for only 3/139 attempts (2%). By far the largest type of kleptoparasitism used by HG against GBB was stealth kleptoparasitism which constituted 126 out of 139 attempts, roughly 91% of HG on GBB kleptoparasitism. Although the HG is closer in size to the GBB, and there may be some HG that can occasionally attempt to use aggression to steal from GBB, on the whole, the superior size of the GBB relegates HG to mostly attempting to steal from them using stealth kleptoparasitism, which as stated before is a less risky but also less profitable strategy.

GBB attempted to kleptoparasitize other GBB in the remaining 94/241 incidents, or 39% of the time that GBB were hosts. Again this is higher than might be expected given the proportion of GBB in the population, and may be the result of greater association between conspecifics whilst foraging. This is something I will consider further in a later section in this chapter when looking at strength of association between species (5.5.1.7). The type of kleptoparasitism used by GBB to steal from GBB differed from that used by the smaller species. Of the 94 occasions GBB were host to kleptoparasitic attempts by other GBB 76 out of 94 (80%) were aggressive kleptoparasitism, and the remainder 18/94 (20%) were stealth kleptoparasitic attempts. This bias towards aggressive kleptoparasitism likely reflects the greater parity in size and strength between individuals within the same species, whilst still also reflecting some competitive differences between individuals within the GBB population as mentioned in section 5.5.1.1.

An examination of the response of GBB hosts to kleptoparasitic attempts at Billingsgate (Table 5.6) showed that GBB hosts surrendered to kleptoparasitic attempts by other GBB on 37/62 occasions, or 59% of the time. Of these 37 incidents a GBB surrendered to aggressive attacks on 33 of these occasions, approximately 89% of the time. This high number reflects the fact that the majority of conspecific kleptoparasitism between GBB was aggressive kleptoparasitism rather than representing an overall unwillingness to defend against aggressive attacks. Those individuals choosing to surrender against conspecifics probably did so based on an individual assessment of the competitive ability of their opponent or the value of the food item being contested regardless of the kleptoparasitic strategy used.

GBB hosts surrendered against kleptoparasitic attacks by HG on 27/60 occasions when they were attacked. This represents about 45% of the incidents where GBB were targeted by HG. The vast majority of these interactions, 25/27, or 93% were stealth kleptoparasitic attempts. As stated before stealth kleptoparasitism is a quick strategy to execute and is difficult to defend against. GBB surrendered against stealth by HG 50% of the time and defended against it 50% of the time (Defend:

26 incidents; Surrender: 25 incidents). Those occasions when they surrendered likely represent events where it was not possible or even beneficial to attempt to defend against the attack.

On the few occasions where GBB were targeted by BHG kleptoparasites GBB defended 100% of the time. As described above all kleptoparasitic attacks by BHG where it was possible to attribute a response by the GBB host were instances of stealth kleptoparasitism, this was only 6 events. This lack of kleptoparasitic interaction clearly representing a lack of a shared foraging niche due to the size difference between these species.

5.5.1.3 – Kleptoparasitism committed by HG at Billingsgate: Table 5.4 shows that HG committed 378 out of 595 (64%) of the kleptoparasitism that occurred at Billingsgate. This clearly accounted for the majority of kleptoparasitism at the site, but was actually slightly less than might be expected given that HG compose 72% of the foraging population. The majority of that kleptoparasitism was committed by juvenile HG's, who accounted for 291 of the 595 kleptoparasitic incidents, or about 49% of the total kleptoparasitism observed. Juvenile HG were in fact responsible for 77% of the kleptoparasitism committed by HG, this was disproportionately high given that they made up only 44% of the HG population at Billingsgate. Juvenile HG also composed 39% of the total population at Billingsgate, so these figures indicate that they committed a disproportionate amount of kleptoparasitism. This would appear to agree with previous literature, which has suggested juvenile gulls may compensate for their lack of foraging skill by attempting to steal more of their food (Verbeek, 1977a). HG adults and sub-adults both committed proportionally less kleptoparasitism than might be expected based on their numbers in the population. HG adults were responsible for 8% of the kleptoparasitism committed at Billingsgate, and sub-adults were responsible for 7%, their percentage composition of the population being 19% and 14 % respectively. As foraging skill develops with age in gulls (Verbeek, 1977a) it might be speculated that although these age groups committed less kleptoparasitism than juveniles they might be better at it and experience more success in the kleptoparasitic attempts they did make. However, this was not the case, and there was no definite pattern of success rate differences between HG age-classes. HG adults had more success with kleptoparasitism than the other two classes, successfully winning 75% of the kleptoparasitism they attempted, but this was not greatly different to the rate of success experienced by juveniles (69%), and juveniles were actually more successful than sub-adult birds, who were successful in 62% of their kleptoparasitic attempts.

The type of kleptoparasitism committed by HG was split largely between aggressive and stealth kleptoparasitism. As stated above, HG were responsible for 378 of the 595 total kleptoparasitic incidents observed at Billingsgate, of these, 180/378, about 30% of total kleptoparasitism, were aggressive kleptoparasitism, and 180/378, also 30% of total kleptoparasitism, were stealth kleptoparasitic attempts. Again, very little scramble kleptoparasitism was observed, only 18/378 incidents which accounted for about 3% of total kleptoparasitism. The use of kleptoparasitic strategies had a clear pattern. The majority of aggressive kleptoparasitism committed by HG was directed towards other HG, 153/180 incidents (85%), with aggressive kleptoparasitism being attempted against GBB on only 10 out of 180 occasions (5.5%).

In contrast, of the stealth kleptoparasitism committed by HG, 126 out of 180 incidents (70%) were directed towards GBB, the remaining 54/180 (30%) being directed towards other HG. This difference in the type of strategy used obviously reflects differences in competitive ability and dominance between the two species. As was seen with GBB the use of an aggressive strategy is clearly being utilised by HG against opponents of equal or lower competitive ability; on the whole, stealth is being used largely against individuals of greater size and competitive ability, and on some occasions against conspecifics, which may represent within-species differences in competitive ability. HG attempted kleptoparasitism against BHG on only 17/378 occasions and in all instances aggressive kleptoparasitism was used against this smaller species. As with interactions between GBB and BHG, this low level of kleptoparasitism against BHG likely reflects a lack of competition over common food resources.

5.5.1.4 – Kleptoparasitism with HG hosts at Billingsgate: HG were the hosts for 53% of the total kleptoparasitism observed at Billingsgate (Table 5.5), this is much lower than the percentage of the population made up by this species (72%), and accounted for 317 of the 595 total kleptoparasitic incidents recorded at the site. Juvenile HG were the host for 35%, adult HG for 14%, and sub-adult HG 5% of the total kleptoparasitism. All these figures are lower than but do not unduly differ from the percentage composition of the population made up by each age class for this species (adult 19%, sub-adult 14%, juvenile 39% - Table 5.2). As was the case with GBB it cannot be concluded from these results that juvenile HG were disproportionately the victims of kleptoparasitism, and there appears to be no significant difference in the extent to which each age-class was kleptoparasitized.

HG were targets of kleptoparasitism by GBB for 94/317 incidents (29%), other HG on 222/317 occasions (70%), and BHG on only one occasion (<1%). On the only occasion that a BHG attempted to steal from a HG, this was using stealth kleptoparasitism. In-keeping with the patterns observed for the other two species, stealth kleptoparasitism again appears to be a strategy used when trying to complete with larger, more dominant individuals. For 29% of the kleptoparasitism experienced by HG, the parasite was a GBB. This is much higher than the expected proportion based on population composition (GBB 12%), and nearly all of these interactions were aggressive kleptoparasitism (91/94). As discussed above, in the section on GBB, this disproportionate use of kleptoparasitism indicates the importance of kleptoparasitic strategies for foraging GBB at Billingsgate. The largest proportion of kleptoparasitism experienced by HG was committed by other HG's. This accounted for 222/317 incidents, or just over 70% of the occasions when HG were hosts. On the majority of these occasions 153/222 (69%) the host was the victim of aggressive kleptoparasitism, for 54/222 incidents (24%) stealth kleptoparasitism was used, and the remaining 15/222 (7%) occasions were incidences of scramble competition. This use of all three strategies probably reflects the greater equality of competitive ability between individuals of the same species, with aggressive strategies still being effective but less so than when used by GBB against HG. The fact that nearly a quarter of the time HG were hosts to the stealth attempts of other HG indicates that these birds are making decisions regarding which strategy to use based on an assessment of the hosts competitive ability and the likely outcome of the attempt.

Scramble kleptoparasitism by HG was experienced 7% of the time HG were hosts. Although this is only a small percentage of the kleptoparasitic activities observed it is worthy of note as it signifies the largest amount of scramble kleptoparasitism that occurred in the Billingsgate population. Scramble kleptoparasitism was very low in frequency at this site. This may be because it is a more complex behaviour to execute as it requires the coordinated and simultaneous action of several individuals. Its absence in the other species but presence, at low levels, in HG at Billingsgate may be the result of stronger foraging association between conspecifics; frequent foraging together at close quarters, and in sufficient numbers, may provide the conditions for some instances of this behaviour to occur.

Where strategies of response could be attributed to HG hosts it was found that HG surrendered food items when attacked by GBB kleptoparasites on 44/45 occasions (Table 5.6). This represents approximately 97% of attacks on HG by GBB. Of these 44 incidents where HG surrendered 41/44, or 93% were aggressive attacks by GBB. This was a predictable result as the majority of kleptoparasitism committed by GBB against HG was aggressive kleptoparasitism and the disparity in size and competitive ability between these two species makes it less likely that a HG would defend against an aggressive attack by a GBB. This is in-keeping with one of the research aims addressed by study 2, as described in the analysis above (Section 5.5.1.3) at the species level HG used a greater proportion of stealth kleptoparasitism against GBB who are the competitively more dominant individuals in the population. Conversely when acting as hosts HG surrendered food items without a fight to that same groups of dominant individuals. This appears to be a demonstration of the Marauder strategy (Broom et al. 2008) or strategy X (Maynard Smith, 1982) being used by a group of subordinate foragers to compete for resources against more dominant individuals.

HG hosts surrendered food items without a fight on 62 out of the 138 occasions they were attacked by other HG. This represents 45% of the occasions where a response strategy could be attributed to the host. Interestingly, this figure matches the percentage with which GBB hosts surrendered food items to conspecifics and, as with interactions between GBB conspecifics, the majority of food items surrendered by HG from HG attacks were the result of aggressive kleptoparasitic attempts, with 51/62 items being surrendered to aggressive attacks, or about 82%. Again, this reflects the fact that a large proportion of conspecific kleptoparasitic attacks committed by HG were aggressive attacks rather than revealing some tendency to surrender more when attacked by HG using aggressive kleptoparasitism.

It was only possible to attribute a response strategy to a HG host on one occasion when it was attacked by a BHG. On that occasion the BHG attacked using a stealth strategy and the HG defended against the attack. With only one data point little meaningful interpretation can be made of any possible patterns in the data regarding interactions between BHG kleptoparasities and the behaviour of HG hosts.

5.5.1.5 – Kleptoparasitism committed by BHG at Billingsgate: BHG composed 16% of the foraging population at Billingsgate but were responsible for only 5% of the total kleptoparasitism committed (Table 5.4). This represents only 28 of the 595 kleptoparasitic events observed at Billingsgate (Table 5.3). This dearth of BHG kleptoparasitism is apparently a reflection of the BHG's smaller size and overall inability to compete for resources with the other two much larger species. The majority of BHG kleptoparasitism, 24/28 incidents (86%), was committed by adults. Adults constituted the majority of the BHG population (95%), so these figures are unsurprising. The kleptoparasitic strategies used by BHG were split 50:50 between aggressive kleptoparasitism and stealth kleptoparasitism. As can be seen from Table 5.4, adult BHG had a much higher success rate in the use of kleptoparasitism than juveniles, with adults winning 92% of the kleptoparasitism they attempted and juveniles only 50%. However, it is unlikely that this accurately reflects a real difference that might exist between the BHG age-classes. There were so few kleptoparasitic incidents involving juvenile BHG that the 50% success rate observed could have occurred by chance. From this it is not possible to say whether or not there is a difference in success rates between BHG age-classes.

A distinct pattern in the way that kleptoparasitic strategies were utilised was apparent in the behaviour of BHG. Stealth kleptoparasitism was the only strategy used by BHG against the larger two study species, this accounted for 9 out of 28 incidents (32%) of kleptoparasitism committed by BHG. As per the comments made above in relation to HG and GBB, stealth kleptoparasitism again seems here to be a less risky strategy that is attempted occasionally by subordinate birds to try and steal from more powerful individuals and species. Kleptoparasitism committed by BHG against other BHG constituted 19 out of the 28 incidents (68%) of BHG kleptoparasitism; this was split between stealth and aggressive kleptoparasitism. The largest proportion committed against other BHG was aggressive kleptoparasitism 74% (14/19 incidents), with stealth making up the remaining 26% (5/19). This mixture of a large percentage of aggressive kleptoparasitism and a smaller but noticeable portion of stealth kleptoparasitism seems to be typical of the kleptoparasitic interactions between conspecifics in all three of the study species at Billingsgate; and, as I have already stated for GBB and HG, appears to demonstrate the tension between a greater equality of competitive ability within-species, whilst reflecting some differences in dominance and competitive ability between some individuals of the same species. The kleptoparasitism of BHG at Billingsgate suggests that this species largely avoids interactions with the GBB and HG. This may mean that BHG seek to forage separately from those species, this is a question to be considered through a strength of association analysis (section 5.5.1.7.

5.5.1.6 – Kleptoparasitism with BHG hosts at Billingsgate: BHG were the hosts of kleptoparasitism for only 6% of the kleptoparasitism observed at Billingsgate (Table 5.5), accounting for 37 of the 595 kleptoparasitic incidents that were recorded in total. This is again much lower than might be expected given that BHG constitute 16% of the foraging population. For 32 out of 37 of these incidents (86%) the victim was an adult bird. This is less than the 95% of the BHG population that adults compose, but does not appear to differ unduly and the differences are not significant enough to conclude that juvenile birds are being preferentially targeted by kleptoparasites.

BHG were targeted by GBB on only 1 occasion, which constituted roughly 3% of the time they were hosts; on 17 of the 37 occasions (46%) that BHG were hosts the species of kleptoparasite was HG, and the largest parasite of BHG was other BHG, making up 19 out of the 37 (51%) attempts to steal from BHG. The vast majority of this kleptoparasitism, 32 of 37 incidents (86%), was aggressive kleptoparasitism, this included all the attempts made by the larger two study species and 14/19 (74%) of the attempts by BHG. Stealth was the only other strategy used against BHG, and as discussed in the previous section this was all committed by other BHG.

The small size of the BHG, and its lesser competitive ability compared to the larger gull species at Billingsgate perhaps make it surprising that this species was not the victim of much more of the kleptoparasitism that occurred at the site. As alluded to previously, the BHG may avoid resource competition with these larger species by taking much smaller prey items, and by trying to forage away from these larger birds. This may account for why more kleptoparasitism towards BHG was not observed. Realistically, BHG conspecifics are the only individuals that this species can effectively exploit through kleptoparasitism at Billingsgate, and the patterns of kleptoparasitism, which BHG committed and were hosts to, shows that this was indeed the case.

An examination of the response of BHG hosts to kleptoparasitic attacks (Table 5.6) showed that they surrendered food items 100% of the time when attacked by the larger two species. This included the one occasion that BHG were attacked by GBB and 7 attacks by HG for which a response could be attributed to the BHG host. All of the attacks by these larger two species were aggressive kleptoparasitic attacks. As described above stealth kleptoparasitism was the only strategy used by BHG against the larger two species, combining this with the fact that BHG surrendered all food items when attacked by HG and GBB provides further support for the possibility that the Marauder strategy described by Broom et al. (2008) is captured by the behaviour of subordinate foragers who use stealth kleptoparasitism against larger, more dominant species but then surrender food items to those dominant individuals if subsequently attacked by them.

BHG surrendered to kleptoparasitic attacks by other BHG on 8 out of 10 occasions that they were hosts. This represents about 80% of attacks for which a strategy could be identified for the host. This is much higher than the rate at which the larger two species surrendered against conspecifics, however, the small number of data points for BHG (10) makes it difficult to ascertain if this reflects a true species difference in behaviour or is just the result of a small sample size. On the occasions where BHG surrendered 7/8 or 88% were to aggressive kleptoparasitic attacks. This is slightly higher than the rate at which BHG used aggressive kleptoparasitic strategies against conspecifics but, when combined with the small number of incidents for which there is data, is not unduly higher to allow conclusions to be drawn about the tendency of BHG to surrender to aggressive kleptoparasitism.

5.5.1.7 – Strength of association: As described in the results in section 5.4.1.3, no significant relationship was found between the extent to which species associated whilst foraging and the amount of kleptoparasitism occurring between those species. This was particularly true of the association between BHG and the larger two species. BHG at Billingsgate would forage alongside

GBB and HG with little kleptoparasitism used against them. The strength of association between BHG and GBB was 38% of patches in common, with only 4% of the kleptoparasitism committed by these two species being directed against each other. Likewise, BHG and HG shared 61% of patches in common, and kleptoparasitized each other on only 4% of all occasions that both species used kleptoparasitic behaviours. This is likely the result of differing food choices and priorities between these species within the same patch. Although BHG shared the same patches with the other species they appear to have occupied a separate niche which has reduced competition between them and the larger species, meaning there was little competitive exclusion of BHG. The limited size of the foraging area and the discrete location of food patches at Billingsgate makes it likely that species that would normally avoid each other, or at least forage apart, may be forced to share the same patch. The BHG seems to be able to do this at Billingsgate as it can exploit different food sources to those preferred by larger gull species. Although the average size of food items sampled and obtained by the different species was not recorded in this research, the difference in bill size between the BHG and the other study species indicates that the BHG will have greater success in handling smaller food items, and being of smaller size could also meet its energy needs through these smaller food items.

The extent to which age-classes at Billingsgate associated whilst foraging was significantly positively correlated with the amount of kleptoparasitism between individuals of those age-classes ($r=0.84$, $p=0.02$). These results suggest that at Billingsgate birds assorted by age-class whilst foraging, and that foraging associations were stronger between same-age individuals. Amongst subordinate individuals, such as juveniles, this may represent an attempt to forage alongside individuals with whom they are more competitively equal, and avoid more dominant individuals. By such behaviour they would be making their chances of successfully defending or stealing food from other patch members more likely. It is also worthy of note that patches containing juveniles had the highest rates of kleptoparasitism within them, this includes those shared with sub-adult and adult birds, suggesting that it was not just juvenile birds joining patches to steal from other juveniles, but sub-adults and adults did this also. This may reflect the fact that the foraging and handling skills of gulls develops with age (Verbeek, 1977a), perhaps making juvenile gulls an easier target for would-be kleptoparasites. An examination of the figures in Table 5.22, supports this idea by showing that all three age-classes committed more kleptoparasitism against juvenile birds than against any other age-class. The figures shown in Table 5.22 are a summary of the data shown in Table 5.3 generalised by age categories.

Table 5.22. Frequency of kleptoparasitism committed by each age-class (rows) and hosted by each age-class (columns) at Billingsgate. Gulls of all three age-classes stole more often from juveniles than from any other age-class. The highest score in each row is highlighted in bold.

	Host: Adult	Host: Sub-adult	Host: Juvenile
Kleptoparasitism: Adult	49	6	**55**
Kleptoparasitism: Sub-adult	14	2	**39**
Kleptoparasitism: Juvenile	95	34	**291**

As juvenile birds were the most populous age-class at Billingsgate (48%), it could be argued that it follows trivially that juvenile birds would both commit more kleptoparasitism than any other age-class, and also be the host to more kleptoparasitism. This was the case at Billingsgate, where juveniles were hosts to 63% of the kleptoparasitism, and responsible for committing 71% of the kleptoparasitism. However, if adopting such a line of reasoning, that the patterns observed simply reflect the abundance of different groups in the population, we should thereby expect to find a more pronounced effect of this nature when considering species, particularly the HG population. HG constituted 72% of the Billingsgate foraging population, but they were hosts to only 53% of the kleptoparasitism that occurred and committed 64% of the kleptoparasitism that occurred. What this tells us is that when looking at the relationship between kleptoparasitism and age-class, juveniles both committed and hosted more kleptoparasitism than might be predicted by the prevalence of this age-class in the population; in contrast, when looking at the relationship between kleptoparasitism and species, HG committed and hosted less kleptoparasitism than might be expected given their prevalence in the population. These patterns concur with the relationships highlighted by the correlational analyses, described in section 5.4.1.3, which indicate that kleptoparasitism at Billingsgate reflects the extent to which age-classes associated whilst foraging rather than the extent to which species associated whilst foraging, and that juvenile birds were preferentially targeted by all age-classes at Billingsgate.

5.5.1.8 - Kleptoparasite and host comparison by species age-class: The use of a single score for each species age-class to compare kleptoparasitism and host rate, whilst controlling for population composition, meant that there was insufficient data for any meaningful inferential statistical analyses to be conducted. However, a visual examination of the data (Figure 5.1) did reveal some interesting patterns. First, the rate at which GBB committed kleptoparasitism and were hosts to kleptoparasitism was much higher than the other species. This was in agreement with the general patterns for GBB at Billingsgate, already described in sections 5.5.1.1 and 5.5.1.2, which indicated that GBB were disproportionately high users and hosts of kleptoparasitism. For all GBB age-classes the rate at which they were hosts was equal to (sub-adult GBB) or higher (adult and juvenile GBB) than the amount of kleptoparasitism they committed. This may be explained by the fact that GBB controlled a lot of the

resources at Billingsgate. Being the largest and most powerful gull species, GBB could obtain most of their food through aggressive kleptoparasitism. Many of the patches at Billingsgate consisted of only a small number of discrete food items, so, once a patch had become established a GBB could join the patch, take control of the food items within it and leave the other foragers with little choice than to attempt kleptoparasitism against that GBB controlling the food, if they wanted to try and gain a share of resources.

Second, within each species juveniles were hosts of kleptoparasitism at a higher rate than any other age-class. This confirmed the results discussed in section 5.5.1.7 which indicated that juveniles of all species were preferentially targeted by kleptoparasites, some reasons for which, such as competitive inequalities linked to maturation, have already been outlined.

5.5.1.9 – Kleptoparasitism by Dominant and Subordinate foragers: To test some of the main patterns of kleptoparasitic behaviour described in the Billingsgate population, analyses were conducted where birds of different species and age-classes were categorised into one of two status groups (Dominant or subordinate). Using these broad categories made it possible to use inferential statistical tests that were not possible for more fine-grained categorisations of individuals by species and age-class, some of which had very few data points.

The two analyses conducted assessed differences in success and failure and differences in the use of aggressive and stealth kleptoaprasitism between dominant and subordinate birds. The small frequency of scramble kleptoparasitism meant this strategy was excluded from the analysis.

The analyses showed that, at Billingsgate, dominant birds (section 5.3.6) were more successful in their use of kleptoparasitism. This result contradicts what was observed within species where no significant differences in success rate were observed between age-classes. However, there were differences between species in success rate, for example, interrogation of Table 5.4 shows that GBB as a species had a mean success rate of 77%, whereas HG had a mean success rate of 65.5%. With the exception of HG adults that were classified as dominant birds along with GBB, these two species largely fell into different status groups and it is likely the case that this significant association between status and success is capturing differences at the species level.

Dominant birds were also significantly more likely to use stealth kleptoparasitism. These findings confirm the patterns of behaviour already described in this chapter for Billingsgate, where more dominant individuals such as GBB, were more likely to use aggressive strategies and subordinates used stealth particularly when trying to steal from species larger than themselves.

5.5.2 – Brancaster:

5.5.2.1 – Kleptoparasitism committed by GBB at Brancaster: GBB were responsible for 6% of the total kleptoparasitism observed at Brancaster. This accounts for 6 of the 98 incidents observed at this site, and is more than twice the rate of kleptoparasitism that might be predicted for this species given that they make up only 2.5% of the total foraging population. Again, this seems to indicate that kleptoparasitism is an important foraging strategy for GBB (section 5.5.1.1). The majority of GBB kleptoparasitism was directed towards HG, this accounted for 4 out of 6 attempts, and on the remaining two occasions the targets were a GBB and a CG. The majority of this kleptoparasitism, 5 out of 6 incidents, were the actions of adult GBB, with the remaining instance of kleptoparasitism committed by a juvenile GBB. No kleptoparasitism by sub-adult GBB was observed. This lack of any data points for sub-adults and the low level of kleptoparasitism by juveniles is likely the result of these age-classes being present at very low numbers in the population, making their behaviour infrequently observed, as opposed to reflecting a general lack of use of kleptoparasitic behaviours by these age-classes. All of the kleptoparasitism committed by GBB was aggressive kleptoparasitism. The level of success experienced by the age-classes was high, with adults being successful in 80% of the attempts they made, and juveniles 100%. This difference in success rate between adult and juvenile GBB is also unlikely to reflect a real difference between age groups, as the juvenile data is based on only one kleptoparasitic event, so no conclusions about the successful use of kleptoparasitic behaviour by different GBB age-classes can be inferred. With only one data point for juveniles the only possible success probabilities were one or zero, making the juvenile success data essentially uninformative.

5.5.2.2 – Kleptoparasitism with GBB hosts at Brancaster: GBB were hosts for only one kleptoparasitic attempt at Brancaster. This was an adult GBB attempting to steal from a juvenile GBB, using aggressive kleptoparasitism. The lack of any significant attempts to steal from GBB is probably a reflection of the small number of this species in the population at Brancaster, meaning they are infrequently encountered, and the fact that they are the largest, and thereby most dominant, gull species. For an individual looking for kleptoparasitic opportunities there are easier targets to challenge than GBB.

An investigation of the rate at which GBB defended and surrendered food items at Brancaster (Table 5.16) revealed that in only one case could a response be attributed to a GBB host. On this occasion that GBB host defended against an aggressive attack by another GBB. As stated in the above paragraph the overall lack of kleptoparasitic attacks on GBB is likely due to their dominance in the foraging environment.

5.5.2.3 – Kleptoparasitism committed by HG at Brancaster: HG were responsible for 41% of the kleptoparasitism observed at Brancaster, this accounted for 40 of the 98 incidents that occurred. This is 6% higher than the percentage of the population composed by this species, but does not appear significantly different to permit the conclusion to be made that this species commits an excessive amount of the kleptoparasitism at the site. Just over half, 21 out of 40 (53%), of these incidents were

committed by juvenile HG's. This is much higher than would be predicted based on the number juvenile HG in the population, which was calculated as 8%. Only one kleptoparasitic incident was committed by a sub-adult HG (1/40), and the remaining 18 out of 40 (45%) were committed by adults. HG adults made up 25% of the total population, so, in contrast to juvenile HG this age-class was responsible for less kleptoparasitism than might be predicted based on their share of the population. The results showed no difference in the level of success experienced between the age-classes when using kleptoparasitism. HG adults were successful 72% of the time, and juveniles 71% of the time, this is excluding the data for sub-adults for whom there was only one data point and therefore no valid way of assessing the actual success of sub-adults when using these strategies at Brancaster.

Almost all of the kleptoparasitism used by HG was aggressive kleptoparasitism (38/40 incidents), and this was directed mostly towards other HG of all three age-classes. HG juveniles attempted an equal amount of kleptoparasitism between adults and other juveniles, who were both the focus of eight attempts each. Given the large proportion of adults to juvenile HG in the population this would suggest that juvenile HG were disproportionately stealing from each other. This may be the case as a pair of juveniles are likely to be similar in their level of competitive ability, and therefore more likely to challenge each other; but it may also be the result of assortment by age-class if juvenile non-breeding birds tend to aggregate together. Both of these explanations are plausible, and the effect observed is likely a combination of these factors. The other two kleptoparasitic incidents by HG were stealth kleptoparasitism. These were both attempts by juvenile HG to steal from other juvenile HG. Again, as stated in previous sections of this chapter, this suggests that stealth kleptoparasitism may be a strategy utilised by individuals of lower competitive ability, sometimes to steal from more dominant individuals, but also, sometimes, to steal from others in the same age-class and species that might be more dominant animals. The only other species targeted by HG was the CG, this accounted for 9 out of the 40 kleptoparasitic attempts by HG, or about 23%. On all these occasions aggressive kleptoparasitism was used against the CG which is a smaller species. This occasional kleptoparasitism of CG may suggest that these two species more frequently forage together, this is something I will investigate further when looking at the relationship between foraging association and kleptoparasitism in a later section.

5.5.2.4 – Kleptoparasitism with HG hosts at Brancaster: HG were the hosts of kleptoparasitic attempts on 37 occasions. This aligns closely with their percentage abundance in the population (35%), so based on these figures they were not unduly targeted by kleptoparasites. On four occasions HG were host to attempts by GBB, and on two occasions by CG. One of the attempts by CG was an attempt to use aggressive kleptoparasitism against an adult HG. This attempt was unsuccessful and probably highlights why aggressive kleptoparasitism is a strategy not used against larger more dominant individuals. On the majority of occasions when HG were hosts, the parasite was another HG, this accounted for 31 of 37 kleptoparasitism incidents, nearly all of which (29/31) were instances of aggressive kleptoparasitism. The other two incidents being stealth kleptoparasitism attempts by juvenile HG as discussed in section 5.5.2.3.

Where a response strategy could be attributed to HG hosts (Table 5.16) it was found that HG surrendered 100% of the time against GBB. This was a total of 4 attacks on HG by GBB, all 4 attacks were aggressive kleptoparasitism which matches previously described patterns seen at Billingsgate where smaller species do not defend food items when attacked by larger species.

A strategy could be attributed to HG hosts attacked by HG kleptoparasites on 27 occasions. Of these 27 kleptoparasitic attempts HG surrendered on 20 of the interactions. This represents a 74% rate of surrender and all 20 instances were aggressive kleptoparasitism attacks. This seems like a high rate of surrender against aggressive conspecific kleptoparasitism but the majority of kleptoparasitic attacks experienced and committed by HG at Brancaster (95%) were aggressive kleptoparasitic attacks so this finding should not be considered unusual. HG were only subject to 2 attacks by smaller species, as stated above these were both attacks by CG and it was not possible to ascertain the response of the HG host for either of these attacks.

5.5.2.5 – Kleptoparasitism committed by CG at Brancaster: CG committed 24% of the kleptoparasitism observed at Brancaster. This does not differ from the level of kleptoparasitism that might be expected given the population composition, of which CG constituted 26%. CG were responsible for 24 attempts to steal food, and nearly all of these were the actions of adult birds, who committed 22 out of 24. This is unsurprising given that 98% of the CG population at Brancaster were adult birds. Aggressive kleptoparasitism was the strategy used on 21/24 occasions, with only one instance of stealth kleptoparasitism, and two scramble kleptoparasitism events recorded. The actual success rate for adult CG at Brancaster was very low, only 45% of attempts were successful. This may result from a greater association between the CG and a number of other species whilst foraging, something that will be investigated in more detail later (5.5.2.9). This low level of success for adult CG, when using kleptoparasitic strategies, cannot however be validly contrasted with the level of success for juvenile CG at Brancaster, which was 100%. The data for juvenile CG was a record of only two incidents, both of which happened to be successful, with such a low number this could have occurred by chance and is unlikely to truly reflect the level of success juvenile CG at Brancaster experience when using kleptoparasitism.

CG attempted to steal from a larger species on only two occasions, these were both attempts to steal from HG. BHG were the target of theft by CG on 8 occasions out of the total 24, on all such occasions the type of kleptoparasitism used was aggressive kleptoparasitism, as the BHG is a slightly smaller species than the CG this fits with the general pattern of behaviour seen at this site and Billingsgate, whereby aggressive strategies are largely employed against smaller species against whom the chance of success is high, and the risk of injury is low. Most CG kleptoparasitism was directed at other CG, this accounted for 14 out of 24 attempts, or 58% of the total kleptoparasitism committed by CG. Most of this was aggressive kleptoparasitism (12/14) which probably reflects the greater parity in competitive ability between individuals of the same species seen elsewhere. The two instances of scramble kleptoparasitism used by CG to steal from other CG may also be the consequence of a stronger foraging association between conspecifics, in a way similar to that discussed for HG at Billingsgate (section 5.5.1.4).

5.5.2.6 – Kleptoparasitism with CG hosts at Brancaster: The CG was the host of attacks by kleptoparasites on 27 occasions, this was about 28% of the total kleptoparasitism observed at Brancaster, and is close to the percentage with which CG occur in the environment (26%), suggesting that as a species they were not disproportionately targeted by kleptoparasites. CG was the only species at Brancaster that experienced kleptoparasitism from all of the study species, which perhaps suggests that it is less selective about the species that it forages near, and goes to no great length to avoid other foraging species. Of the kleptoparasitic attempts to which it was host, only one was committed by a GBB, and three were attempts by BHG. The three attempts by BHG were all aggressive kleptoparasitism, however, none of these were successful which is likely a result of the slightly larger size of the CG allowing that species to successfully defend its food source against BHG. HG were the parasite for a significant proportion of the occasions when CG were hosts, on 9 of the 27 incidents, all these attempts were aggressive kleptoparasitism, with this strategy again being used by a larger species to steal from a smaller species. These results would seem to indicate that the CG and HG might associate closely when foraging at Brancaster. The majority of times that CG were hosts this was to attempted thefts by other CG, accounting for 14 of the 27 times that CG were the victims of theft, the vast majority of which (12/14) were aggressive kleptoparasitism. Only 50% of these attempts were successful, which is lower than the success rate for larger species when using aggression against conspecifics, suggesting that CG hosts were either effective at defending their food against other CG due to within species asymmetries, perhaps higher quality individuals were the ones already in possession of food; or the types and sizes of food items being competed over were easier to defend.

It was possible to identify a strategy of behaviour for CG hosts for 11 kleptoparasitic events (Table 5.16). On 4 of these occasions CG were attacked by HG, they surrendered 3 times and defended on 1 occasion (75%) and all attacks were aggressive kleptoparasitism. With such a small number of data points it is difficult to provide a meaningful interpretation of the data but the pattern seems to fit with behaviour described previously for this site and for Billingsgate where small species surrender food at a high rate when attacked by larger more powerful individuals.

Only 1 interaction was recorded between BHG and CG hosts for which a strategy could be identified for the host, on this occasion CG defended against an aggressive attack by a BHG, again an example of a larger species defending against a smaller species. CG hosts surrendered on 3 out of 6 occasions when they were attacked by other CG. This represents a 50% probability of CG surrendering against conspecifics and seems an intuitive result given the greater parity of competitive ability likely to be seen within species. All of these attacks were instances of aggressive kleptoparasitism which is unsurprising as the majority of conspecific kleptoparasitism between CG at Brancaster involved aggressive strategies (12/14 or 86%).

5.5.2.7 – Kleptoparasitism committed by BHG at Brancaster: BHG were responsible for 29% of the kleptoparasitism observed at Brancaster. In total this was 28 kleptoparasitic incidents, and, as BHG made up 36.5% of the population, was lower than expected based on the percentage of the population they constituted, but is perhaps not a significantly large enough difference to permit the

conclusion to be drawn that BHG utilise kleptoparasitic strategies less than the other gull species in this environment. Although this is probably the case when competing with other gulls, as the BHG was the smallest of the study species considered in this research, it should be noted that there are other bird species at Brancaster from whom to steal, many of whom would be much easier targets than other gulls. BHG were observed kleptoparasitising wader species, such as sanderling (*Calidris alba*) and greenshank (*Tringa nebularia*), during the study period, and it is surmised that the proportionally low level of BHG kleptoparasitism recorded at Brancaster in this study reflects a tendency for BHG to target species easier to tackle than gulls, and not a general lack of the use of kleptoparasitic behaviours by BHG. Such interspecific kleptoparasitism by BHG has been the focus of previous research by other authors (Barnard & Thompson, 1985).

All kleptoparasitic attempts recorded at Brancaster were attempts by adult BHG. No observations were recorded of juvenile BHG being either the attacker or host of kleptoparasitism at Brancaster, and this is likely a consequence of the fact that they made up only 0.5% of the population, making their presence so small that behavioural interactions involving them were infrequent. Apart from three unsuccessful attempts to steal from CG, all BHG kleptoparasitism was directed towards other BHG, in total 25 of 28 incidents, this likely reflects a greater foraging association between conspecifics. BHG used all three kleptoparasitic strategies against other BHG. The majority of these were aggressive strategies, which were used on 17 out of the 25 occasions, on four occasions stealth kleptoparasitism was used, and on a further four occasions scramble kleptoparasitism was used. This pattern of strategy use, with aggressive strategies used most commonly combined with some use of other less risky strategies, fits in with the behaviour observed in the other study species when targeting conspecifics. BHG had a reasonably high success rate when using aggressive strategies against other BHG, with 11 out of 17 attempts (65%) being successful; but were unsuccessful, in all eight attempts at stealth and scramble kleptoparasitism. Nothing should be inferred from these figures in relation to the BHG's ability to execute stealth and scramble strategies, as the number of data points was so low chance effects cannot be ruled out. The fact that BHG were the smallest study species in this research, and thereby subordinate to the three larger species provides a good indication of why BHG kleptoparasitism at Brancaster was restricted to other BHG.

5.5.2.8 – Kleptoparastism with BHG hosts at Brancaster: BHG were hosts to 33% of the kleptoparasitism observed at Brancaster, this was 33 total incidents. This is larger than the percentage of kleptoparasitism committed by BHG, but is still less than the proportion of the population composed by BHG (36.5%). These results suggest that BHG were not unduly targeted by kleptoparasites due to their smaller size. All attempts to steal from BHG were directed towards adult birds, as stated in the previous section (5.5.2.7) this is due to the lack of juvenile birds at the site as opposed to a specific decision about which individuals to target.

CG attempted to steal from BHG on eight occasions (8/33), all of which were aggressive strategies, and only three were successful. This matches the low level of success experienced by CG when targeting other CG, and, as stated in section 5.5.2.6, may have a number of explanations, such as the size and type of food being competed over and the ease with which it can be defended. The

only other species that tried to steal from BHG was other BHG, all three strategies were used, with the majority of attempts being aggressive kleptoparasitism. Only 11 out of 25 (45%) attempts by BHG to steal from BHG were successful. This is lower than the other three study species, but does not differ significantly from the success rate with which CG steal from other CG, which was also low at 50%. The fact that these two smaller species had much lower success when targeting conspecifics seems to suggest that this effect may be due to some environmental factor, such as the type of food being exploited, as opposed to an inability to effectively wield kleptoparasitic strategies against conspecifics.

Strategies of response for BHG hosts were identified for 23 kleptoparasitic events (Table 5.16). In 15 of these interactions BHG were attacked by other BHG, they defended food items 11 times and surrendered on 4 occasions or about 26% of events. This represents a much lower rate of surrender than seen among the other species when kleptoparasitized by conspecifics and as stated in the above paragraph may reflect the type of food items held by BHG, with small items being easier to defend and consume quickly than larger items held by bigger species. All 4 occasions when BHG surrendered were aggressive kleptoparasitic attempts but, as BHG defended against aggressive attacks on 8 occasions, little can be inferred about the tendency of BHG to avoid protracted fights with conspecifics from these results.

The remaining 8 kleptoparasitic interactions for which the behaviour of BHG hosts could be identified were attacks by CG. All of these attacks were aggressive kleptoparasitic attacks and BHG defended on 4 occasions (50%) and surrendered on 4 occasions (50%). The fact that all these attacks by CG on BHG were examples of aggressive kleptoparasitism is probably a reflection of the slightly larger size of the CG compared to the BHG and conversely the 50:50 split between defending and surrendering against CG may at the same time reflect the fact that although the CG is larger there is not a great size difference between these species making matches between them fairly even.

5.5.2.9 – Strength of association: The degree to which species associated whilst foraging and the rate at which those species kleptoparasitized each other was significantly positively correlated at Brancaster (r_s=0.75, p=0.006). This supported the prediction made for study 2 regarding the relationship at Brancaster between strength of association between species and kleptoparasitism (section 5.2). It was anticipated that the large size of the study area at Brancaster would allow individuals to segregate into foraging groups with preferred compositions. Particularly, it was expected that the smaller gulls (BHG and CG) may forage away from larger gulls (HG and GBB). However, the largest number of patches were mixed patches containing HG, CG, and BHG. Interestingly, within these patches the majority of kleptoparasitism was committed against conspecifics (Table 5.13), with whom, overall, each species was most strongly associated. This trend may represent a tendency by each species to exploit slightly different food sources, or even to segregate by species within a patch. Patches at Brancaster could be quite large as the food sources exploited, being small marine invertebrates, annelids, and crustaceans, were dispersed throughout the environment. The locations of individual species within patches was not tracked in this research but it was anecdotally noted that certain species tend to favour slightly different foraging behaviours. For example, BHG were

frequently observed paddling and plunge-diving in shallow channels. Such differences would cluster individuals together by species within a patch creating greater opportunity for theft from conspecifics. As entry to a patch cannot be controlled and any individual can join, an alternative explanation is that more dominant individuals would join patches where they could exploit subordinates, such as HG foraging alongside smaller CG and BHG. However, this apparently wasn't the case because, as stated above, within such patches individuals largely stole from conspecifics. So, HG mostly stole from HG as opposed to targeting potentially easier victims in CG and BHG. The GBB was an exception to this as it stole more food from HG than other GBB. However, the small number of GBB foraging at Brancaster (2% of the foraging population) accounts for this finding, as it meant that the likelihood of encountering another GBB from whom to steal was quite small. In fact there were no patches that contained only GBB.

The extent to which age-classes at Brancaster associated was also strongly correlated with the rate of kleptoparasitism between age-classes (r_s=0.82, p=0.02). However, this was a predictable finding as the majority of the population were adults (88%), and subsequently they were the host and kleptoparasite the majority of the time at Brancaster, with adults being host 81% of the time and committing 75% of the kleptoparasitism that occurred. In fact, only one foraging patch contained no adult birds, making the result of the age-class correlation unsurprising and largely uninformative. From the two correlational analyses conducted for Brancaster, despite both being significant, gulls at Brancaster appear to forage alongside conspecifics within patches and exploit kleptoparasitic opportunities against those same individuals.

5.5.2.10 - Kleptoparasite and host comparison by species age-class: The comparison of kleptoparasitism and host scores for each species age-class was conducted through visual examination of Figure 5.2, as opposed to the use of inferential statistics. The patterns of note at Brancaster, once population composition was controlled for, were that GBB adults committed kleptoparasitism, but were never hosts to kleptoparasitic attempts. This likely reflects their dominance in the foraging environment. The abundance of other food sources and presence of easier targets from whom to try and steal at Brancaster, may make adult GBB an unappealing prospect to try and challenge for food.

Excluding the BHG, for whom there were no data points, juvenile birds were both the parasite and host at a much higher rate than any other age-class. This again suggests that, despite the low rate of kleptoparasitism overall at Brancaster, juvenile birds were preferentially targeted by kleptoparasites. As discussed in relation to a similar finding for Billingsgate, this may well reflect inequalities in the competitive and foraging abilities of immature birds, giving them greater need to use kleptoparasitic strategies as well as being easier hosts to steal from.

5.5.2.11 – Kleptoparasitism by Dominant and Subordinate foragers: As with Billingsgate (section 5.5.1.9), different species and age-classes were categorised as dominant and subordinate a defined in section 5.3.6. This aggregation of data into broad categories allowed inferential statistics to be used to further investigate some of the patterns described for Brancaster in previous sections of this

chapter. Two analyses were conducted: The association between status group and success in the use of kleptoparasitic strategies, and the association between status group and use of aggressive and stealth kleptoparasitism. Again, scramble kleptoparasitism was excluded because of its occurrence at low frequencies.

No significant association was found at Brancaster between success in the use of kleptoparasitism and status, nor was a significant association found between the type of kleptoparasitic strategy used and the status of gulls. In relation to the status and success analysis this finding supports the patterns described within species at Brancaster where no strong indication could be found of a difference between age-classes of the extent to which kleptoparasitism was successfully used. However, the lack of a significant association between status and type of kleptoparasitic strategy used differed from expected at Brancaster and the finding at Billingsgate, where subordinate individuals used more stealth kleptoparasitism. Stealth was predicted to be a strategy used by subordinate gulls to compete with dominant gulls, however, this was not the case at Brancaster and this may be due to the fact that species at Brancaster seemed to direct their kleptoparasitism more towards conspecifics, with whom they are more competitively equal. Further, the Brancaster dataset was small with few data points for some species and ages. This can be seen from the lack of a frequency score for stealth by dominant birds at that site (Table 5.21).

5.6 – General Discussion

In section 5.5 I interpreted and discussed at length the results of the kleptoparasitism data recorded at Billingsgate and Brancaster. In this section I intend to consolidate that discussion by summarising the most significant results extrapolated from those datasets in relation to the predictions made for this study.

First, the lack of scramble kleptoparasitism in both study environments is worthy of mention. Scramble kleptoparasitism occurred at negligible levels at both Billingsgate and Brancaster. On the whole scramble kleptoparasitism requires the simultaneous coordination of the behaviour of several individuals, and the absence of scramble kleptoparasitism at both sites suggests that gulls perhaps lack the social cognition to be able to coordinate their behaviour to the required level. The absence of scramble kleptoparasitism was most surprising at Billingsgate, where the high density of foragers and the tendency for GBB to dominate established food patches might have suggested it as an effective strategy for subordinate birds to acquire at least some share of the food in a patch, whilst diluting the risk associated with challenging a GBB for food. However, rather than coordinating their behaviour, I noted from my observations of patches, subordinate gulls, particularly HG, would either individually take a chance with stealth kleptoparasitism against a GBB, or they would fight amongst themselves to be in the best position to pick up the remains of any food item that the GBB may leave behind after it was satiated and had finished handling.

The little scramble kleptoparasitism that did occur involved HG stealing from HG at Billingsgate, with CG stealing from CG, and BHG stealing from BHG at Brancaster. I considered the

possibility that these instances of scramble kleptoparasitism, involving conspecifics, might be explained by strong foraging associations between conspecifics producing conditions that promote occasional scramble kleptoparasitism when foraging at close quarters. This seems plausible for HG at Billingsgate who had a strong foraging association, with multiple HG sharing 93% of patches in common, in addition to the overall high forager density at this site. At Brancaster CG and BHG also had a high percentage of patches in common with conspecifics (CG: 61%; BHG: 68%), which in combination with the finding that species at Brancaster may segregate into same species groups within patches (section 5.5.2.9), may account for the pattern of scramble kleptoparasitism seen there.

However, HG had the strongest foraging association with conspecifics at Brancaster, with multiple HG sharing 82% of patches in common, but this species made no use of scramble kleptoparasitism. The size of food items at Brancaster may explain this result. The food at Brancaster was on average much smaller than at Billingsgate, this would mean there were fewer food items that could be shared between multiple individuals, particularly for larger gull species such as HG, perhaps making scramble kleptoparasitism a strategy of less value for HG at Brancaster. The speculations I have made here regarding strength of association being a predictor of scramble kleptoparasitism may provide an accurate account of some of the behaviour observed, however, the main point regarding scramble kleptoparasitism that can be drawn from this research remains the idea that gulls appear to lack the social cognition to make scramble kleptoparasitism anything other than an occasional strategy. This finding supported the prediction (section 5.2) that little scramble kleptoparasitism would be seen in these study populations.

Second, the analyses of the correlation between strength of foraging association and kleptoparasitism produced an interesting result for Billingsgate. The finding that there was a significant correlation between these factors with respect to age-class but not species was surprising, as one species (HG) made up a significant majority (72%) of the foraging population, leading to the assumption that HG would be found together in patches at high rates and steal from each other at high rates. However, this assumption was found to be erroneous, as foraging gulls appeared to associate most strongly by age-class, with individuals of all age-classes joining patches to forage alongside juveniles against whom they could try to exploit kleptoparasitism opportunities.

The tendency for juvenile birds to be the target of more kleptoparasitic attempts than other age-classes held for both Brancaster and Billingsgate, and was confirmed by the analyses conducted to compare differences in the rate at which each species age-class committed and was host to kleptoparasitism. Once the proportions of each age-class in the population were controlled for it was found that juvenile birds were hosts more than any other age-class at both Billingsgate and Brancaster, this was in line with the second prediction made for this study (section 5.2). The fact that foraging and competitive ability develops in gulls as they mature (Verbeek, 1977a) suggests why they might be easier and preferred targets for kleptoparasites.

Third, the kleptoparasitic behaviour of all study species showed some interesting patterns of regularity. Against smaller species than themselves the study species almost entirely used aggressive

kleptoparasitism as a pure strategy. Against study species larger than themselves gulls resorted to using a pure strategy of stealth kleptoparasitism. In contrast, when trying to steal from conspecifics all study species used a mixture of aggressive and stealth kleptoparasitism, with aggressive kleptoparasitism making up the largest percentage of this mixed-strategy.

Considered superficially these results seem obvious and intuitive. A gull attempting to steal from a smaller less-powerful species can most efficiently achieve its ends with little risk by using an aggressive strategy. Alternatively, a gull trying to steal from a larger more-powerful species would be best-off using a stealth strategy, which is quick to execute, difficult to defend against, and will often result in some small payoff while minimising injury and energetic costs from engaging in a lengthy fight. Some of these patterns were verified inferentially for the broad categories of dominant and subordinate birds at Billingsgate. It was found that dominant individuals were more successful kleptoparasites and that they made greater use of aggressive strategies than subordinate gulls, who used more stealth kleptoparasitism. However, the results of these tests for Brancaster were non-significant, showing no difference between status groups in success rate and strategy used. This may be the result of a small dataset for Brancaster but is also likely to be influenced by the limitations of dichotomising species age-classes into two categories. For example, using this allocation juvenile HG were classed as subordinate foragers, however, the status of these birds is not fixed and should be assessed relative to their opponent. So, when attacking BHG and CG juvenile HG would not be subordinate because of their greater size, the same would also apply when attempting some kleptoparasitism against some conspecifics.

When stealing from conspecifics, between whom contests will be more evenly matched, gulls can choose between the two strategies. That choice will be influenced by their assessment of the competitive abilities of the opponent. If the opponent is assessed to be of lower competitive ability than themselves they could use aggressive kleptoparasitism, alternatively they might attempt stealth kleptoparasitism if they are outmatched. When using a mixed-strategy of aggressive and stealth kleptoparasitism the decision as to which type of kleptoparasitism to use will be influenced by the opponent but also by the perceived value of the food being contested.

At Billingsgate gull species used mixed-strategies against conspecifics in a very consistent way. For example, when attempting to steal from GBB conspecifics, on average, GBB used aggressive kleptoparasitism 81% of the time and stealth kleptoparasitism 19% of the time. HG used aggressive kleptoparasitism 74% of the time and stealth 26% of the time when stealing from conspecifics; and BHG used aggressive kleptoparasitism against conspecifics 74% of the time and stealth 26% of the time. This gives a general mix of aggressive and stealth strategies when used against conspecifics in the Billingsgate population of 76% aggressive, 24% stealth, the figures given above are presented in Table 5.23.

Table 5. 23. Mixed-strategies for conspecific kleptoparasitism at Billingsgate. Figures show percentage of time each strategy was used against conspecifics in the general case for Billingsgate and by species.

Conspecific Kleptoparasitism	Aggressive	Stealth
Population	76	24
GBB – GBB	81	19
HG – HG	74	26
BHG – BHG	74	26

The regularity apparent in the mixture of kleptoparasitic strategies recorded for contests between conspecifics at Billingsgate, being about three aggressive incidents to one stealth (3:1), suggests that for the three study species this mixture may have settled on an equilibrium. However, subjecting the data shown in Figure 5.23 to a game-theoretical analysis to see if the probability with which each strategy is used against conspecifics conforms to a Nash equilibrium (Nash, 1951; Chapter 1, section 1.2 and Appendix B) would require, in the general case and for each species, the calculation of average payoffs for each strategy. This would be a function of the value of the resources obtained, the probability of achieving a successful theft with that strategy and the costs incurred by both the parasite and host from any potential fight over the item. Analysing whether conspecific kleptoparasitic behaviour at Billingsgate meets the conditions for a Nash equilibrium would tell us something important, in a restricted sense, about how adaptive the foraging decisions of gulls at Billingsgate are, however, with no direct way of identifying payoffs and costs in these contests perhaps the strongest conclusion that can be drawn from this pattern of behaviour is to make the observation that at a qualitative level conspecific kleptoparasitism at Billingsgate may conform to game-theoretic predictions regarding equilibria and may even be a real world example of a Nash equilibrium in a foraging population.

A further aim of this study was to assess whether stealth kleptoparasitism could be considered to be a real foraging example of the Marauder strategy (Broom et al. 2008), or what Maynard Smith (1982) called strategy X. It was predicted that this strategy may best be described by the kleptoparasitic behaviours of subordinate individuals in the foraging populations. This was considered at the species level as differences in size and strength between species of gull are the most straightforward example of an asymmetry in RHP seen in the study populations. If a subordinate forager uses stealth kleptoparasitism when attacking dominant individuals and subsequently surrenders food items without a fight when attacked by more dominant individuals it was suggested that such behaviour would be a plausible candidate for a Marauder strategy.

As described earlier in this discussion, the study species' resorted to a pure strategy of stealth kleptoparasitism when attempting to steal from larger species than themselves. So, HG used stealth against GBB; CG and BHG used stealth against HG and GBB. This supports the first part of this prediction regarding how subordinate foragers behave when challenging dominant individuals. In addition, it was also found that when hosts of the different study species were attacked by a larger more dominant individual these species would surrender at a high rate, so, HG surrendered when

challenged by GBB; and BHG and CG surrendered when challenged by HG and GBB. These results suggest that the existence of stealth kleptoparasitism creates a useful behavioural option for subordinate birds, meaning that the use of kleptoparasitic strategies is not just a game for dominant individuals and that the use of kleptoparasitism by subordinate gulls in these study populations may provide an empirical demonstration of the use of a Marauder (strategy X) foraging strategy.

5.7 – Summary

In this chapter I have described the data on kleptoparasitism collected at Billingsgate and Brancaster over the period of study. I have interpreted that data to describe patterns of behaviour that were recorded, with the use of multiple kleptoparasitic strategies revealing interesting patterns of behaviour in both study populations. In discussing some of the predictions I have considered how subordinate individuals of different species have tried to use kleptoparasitism to compete for resources.

(6)

Chapter 6 – Study 3: Differences in foraging behaviour between dominant and subordinate gulls at Billingsgate

6.1 – Introduction

In the previous chapter I discussed the results of study 2 which sought to describe the main patterns of kleptoparasitic behaviour seen in the study populations at Billingsgate and Brancaster. In that chapter I spent some time considering how subordinate foragers in those populations might use kleptoparasitism to compete for food resources with more dominant individuals. Differences in dominance status in study 2 were assessed in two ways: at the level of species and age-class, with smaller species and juvenile birds being considered subordinate to larger species and adult birds; and by dichotomising the population into two status categories (dominant/ subordinate). At Billingsgate it was found that subordinate individuals were less successful kleptoparasites and were also more likely to use stealth kleptoparasitism. In this chapter I outline the results of study 3. Study 3 developed this investigation of the differences in foraging behaviour between dominant and subordinate foragers by considering what other behaviours, beyond kleptoparasitism, subordinate gulls might use to compete for resources in the study environment at Billingsgate.

6.2 – Study rationale and predictions

Animals use various foraging strategies to meet their energy requirements and these strategies are influenced by a species social structure and the ecological parameters of the environment in which that species lives and forages. Research has shown that environmental conditions impose both opportunities and constraints on animals and that these act in synthesis with social pressures to influence the evolution of group structure and foraging behaviours (Barnard & Thompson, 1985).

Study 2 examined the main patterns of kleptoparasitic behaviour seen in the study populations for this research, including which individuals used particular types of kleptoparasitism and against whom. That study provided some insights into how subordinate individuals behaved when competing for resources but more analysis was done to develop that picture. Beyond kleptoparasitism, there are a number of other foraging strategies that a subordinate foraging gull could use to compete for food. Identifying and analysing those patterns of behaviour was the focus of this study which addressed the third general research aim outlined for this project.

To gain an understanding of how, and if, the behaviour of subordinate gulls differed from more dominant individuals observations of natural foraging behaviour and a field experiment to manipulate the food items available to foragers were used. The field experiment also involved a novel

piece of apparatus that had to be entered to obtain food. This was used to assess the boldness of foragers and their willingness to engage in risky behaviours.

The focal population was the gull population at Billingsgate. This population was used as the limited area of the study site made it a location more conducive to conducting a field experiment and because the Billingsgate population contained a more diverse mixture of age-classes than Brancaster, which predominantly consisted of adult birds.

In relation to the above research question and rationale, it was predicted that a subordinate gull will forage differently to other gulls at Billingsgate. Specifically, it was predicted that subordinate birds would be first to food giving them a finder's advantage (Giraldeau & Caraco, 2000), that being the opportunity to obtain and consume some food before being displaced by the arrival of dominant birds. To achieve this they were predicted to distribute themselves differently to other gulls around the study site when loafing, keeping themselves closer to likely food sources and locations.

Further, it was predicted that subordinates would have to spend more time foraging, to compensate for poor foraging ability among juveniles and the competitive disadvantages for some individuals of being smaller than other gulls. Last, it was predicted that subordinates would engage in more risk-prone foraging behaviour in order to meet their energy requirements. Subordinates were expected to be more likely to approach environmental novelties in search of food and forage in smaller spaces thereby reducing their flight distance from potential predators.

6.3 – Analyses

Dominance in the foraging gull population at Billingsgate was assessed using two criteria: size and foraging ability, as already outlined in section 3.5.6. To recap, size is a clear indicator of differences in strength between gulls, it is an asymmetry that is readily perceived and will therefore influence the outcome of contests between individuals (Maynard Smith 1982). Foraging ability is something that has been shown to improve in gulls with age and experience up to maturity (Verbeek, 1977a; Bertellotti & Yorio, 2000). Using these criteria the foraging population at Billingsgate was categorised in status as either 'dominant' or 'subordinate'. The dominant category consisted of all three age-classes (adult, sub-adult and juvenile) of Great Black-backed gull (GBB: *Larus marinus*) and adult Herring gulls (HG: *Larus argentatus*). The subordinate category contained sub-adult and juvenile HG and both age-classes (adult and juvenile) of Black-headed gull (BHG: *Chroicocephalus ridibundus*). All age-classes of GBB were considered dominant because of their large size and aggression, even when juveniles; and all age-classes of BHG were considered subordinate because of their smaller size. Using these criteria to divide up the known population composition at Billingsgate, the dominant category made up 40% and the subordinate category made up 60% of the study population.

Four analyses were conducted to investigate differences in foraging behaviour between the dominant and subordinate groups: First, (*Part A*) a comparison was made of the frequency with which the two groups engaged in foraging behaviour to see if one group spent more time engaged in

foraging activities than the other. Second, (*Part B*) the locations where individuals in the two groups loafed at the study site, relative to the main hotspot where food patches occurred, were assessed. Third, (*Part C*) an examination was made of whether subordinate birds try to obtain a share of contested food by getting to food first. Fourth, (*Part D*) an assessment of whether subordinates take more risks to acquire food than do dominant individuals.

6.3.2 – Part A: Is there a difference in the frequency of foraging behaviours between dominant and subordinate birds?

Over the year of study 80 hours and 15 minutes of observations were conducted at Billingsgate. Throughout these observations, data about the population was recorded as headcounts of gulls present at the site at 30 minute intervals. Each headcount recorded the number, species and ages of birds, as well as the location at the site where the bird was recorded. The location was noted as either on the ground in the car park area (Trader's car park was the study area, see Chapter 3 section 3.2.2) or on one of the 5 main buildings around the study site, these buildings are described in the section that follows (6.3.3 – Part B).

This simple dichotomy of location, between 'ground' and 'building', was used to assay frequency of foraging behaviour. Gulls loafed and rested on buildings around the study site and foraged on the ground in the car park where food sources occurred through being dropped or discarded. Gulls did very little loafing or resting on the ground in the car park because this area was busy with both pedestrians and vehicular traffic. The frequency with which birds were recorded on buildings was used as a measure of how much time they spent loafing and the frequency with which birds were recorded on the ground was used as a measure of how often they actively engaged in foraging behaviours. It was predicted that to compensate for their lesser competitive ability and overall poorer foraging ability than dominant birds, subordinate birds would need to spend more time foraging to meet their energy needs and that this would be reflected by the frequency with which subordinate birds were recorded on the ground. A Chi-square analysis was conducted to assess if there was a significant relationship between status group (dominant or subordinate) and frequency of foraging behaviour, measured by birds spending greater time on the ground.

6.3.3 – Part B: Do subordinates loaf closer to foraging patch hotspots?

To assess whether there was a difference in how close subordinate and dominant gulls loafed relative to the most common locations of food it was necessary to measure a number of things: First, the main location in the study area where sources of food were concentrated was identified, this was referred to as the patch hotspot. Second, the mean flight distances to the hotspot from the main loafing areas at the site were calculated.

6.3.3.2 – Identification of the patch hotspot: Over the year that fieldwork was conducted the presence of food patches in the study area was recorded. Data on the time, duration and number of birds exploiting a patch were noted as well as the location of the patch in the study area. Figure 6.1 shows

an aerial photograph of the Billingsgate study site overlaid with a grid system dividing the area into 25m x 19m grid squares. During fieldwork the location of each patch recorded at Billingsgate was marked onto datasheets containing Figure 6.1. An example datasheet is attached at Appendix G.

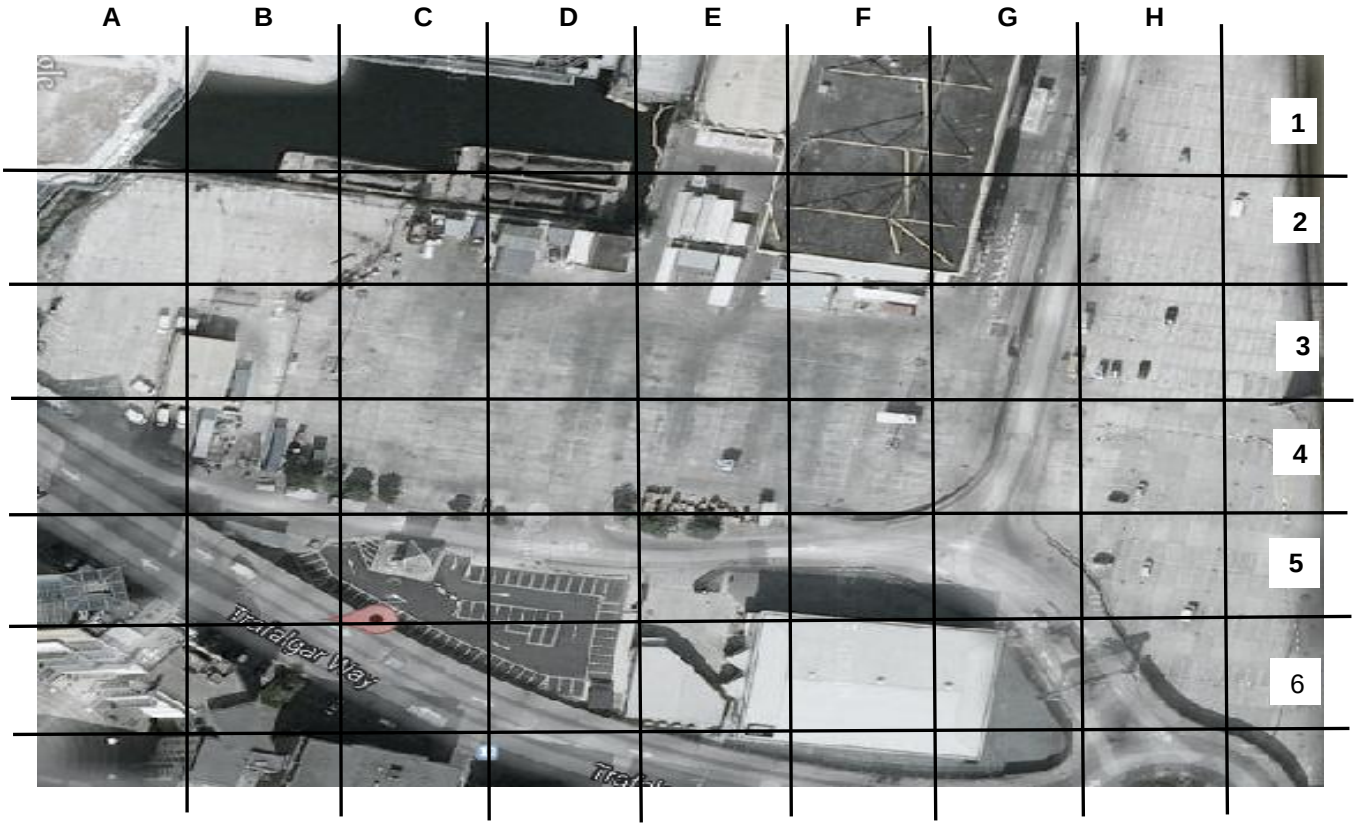


Figure 6.1. Aerial photograph of the Billingsgate study area (Trader's Car Park). Grid squares measure 25m x 19m. Image taken from Google maps on 06/03/14.

A total of 183 patches were recorded at Billingsgate. Figure 6.2 shows the frequency of patches occurring in each grid square. The areas of the study site where patches of food were most likely to occur were grid squares: C3, D3, C4 and D4, with approximately 72% of patches occurring in this region. Of these grid squares C3 and D3 contained the highest number of foraging patches, with C3 containing slightly more patches (44 patches) than D3 (41 patches). As patches were not distributed evenly within grid squares plotting each foraging patch in its relevant position in squares C3 and D3 suggested the centre of a hotspot for foraging patches at the site in the north-east corner of square C3 as shown in Figure 6.3. This was identified as the central place where large amounts of food regularly appeared and fitted well with my personal observations as this point was close to an area where waste and bins at the site were processed and cleaned out, presenting regular opportunities to obtain food in that area. The hotspot identified in Figure 6.3 was the point from which the distances to all loafing areas were measured.

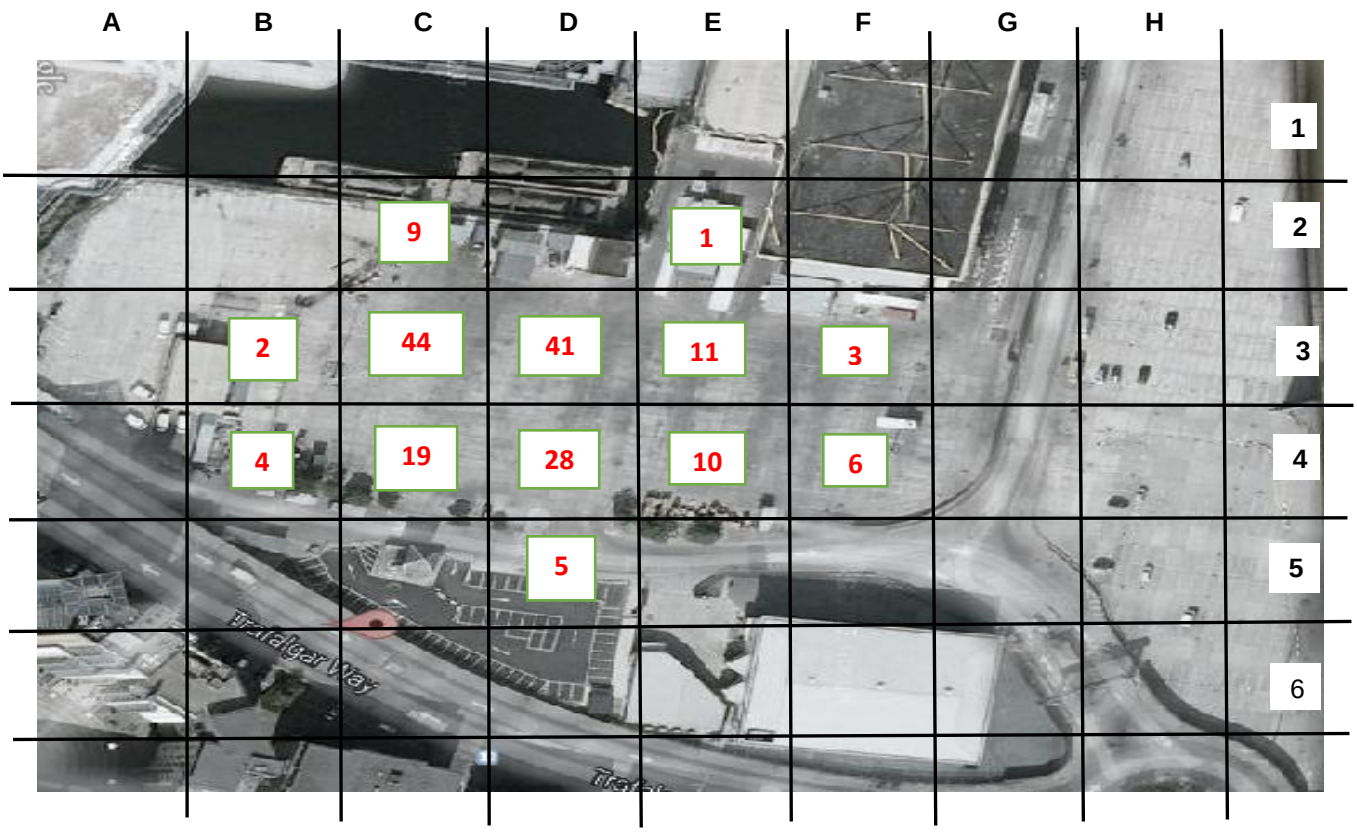


Figure 6.2. Frequency and distribution of foraging patches occurring at Billingsgate. Frequency counts of foraging patches recorded in each grid square are shown in red (N=183). Image taken from Google maps on 06/03/14.

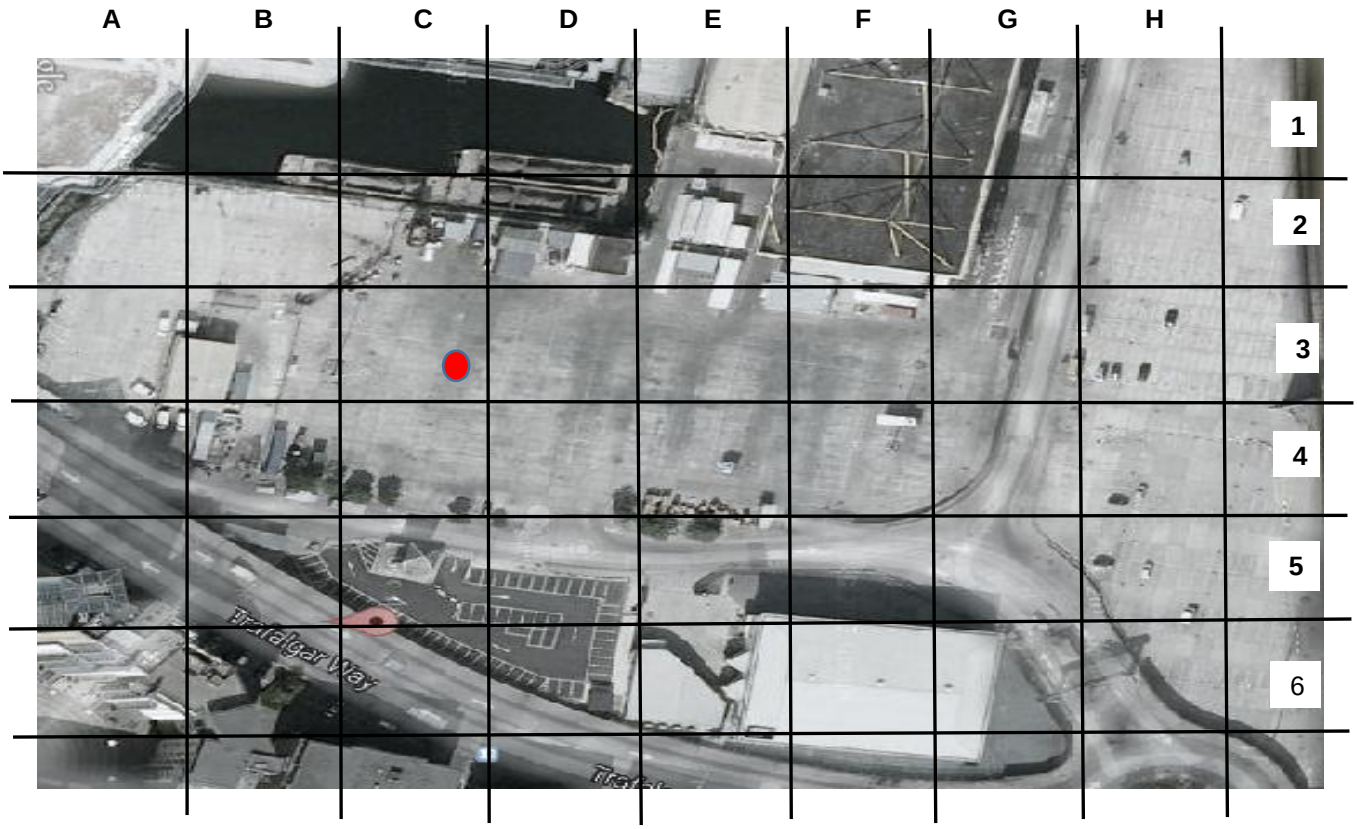


Figure 6.3. Location of the foraging patch hotspot in the Trader's Car Park at Billingsgate. The area marked with a red circle in the north-east corner of grid square C3 was identified as the centre of the area where a large proportion of foraging patches occurred. Image taken from Google maps on 06/03/14.

6.3.3.3 – Mean flight distances from loafing areas to hotspot: Five main loafing areas at Billingsgate were identified, these were the building roofs surrounding the Trader's Car Park, described below and demarcated in Figure 6.4.

- Building 1: The main market building. This consisted of a large flat roofed area adjoining a slightly higher corrugated roof extension. The loafing area on this roof was demarcated by a series of points that marked the boundaries of areas overlooking the hotspot and study area. The boundaries of this loafing area are outlined in red on Figure 6.4.
- Building 2: Consisted of 3 roofs of closely adjacent workshops. The heights of these 3 roofs differed. One roof was flat and two were pitched. The loafing area depicted in Figure 6.4 and labelled as Building 2 consisted of the entire flat roof of one building and the sides of the 2 pitched roofs facing the study area. The boundaries for this loafing area are outlined in blue in Figure 6.4.
- Building 3: Was a fish processing unit south of the study area. This building had a pitched roof. The loafing area of interest was the side of the roof from the north edge of the building to the apex that overlooked the study area as shown in Figure 6.4. The boundaries for this loafing area are outlined in green in Figure 6.4.

- Building 4: Located to the south of the Trader's Car Park near to Building 3, consisted of a flat roofed processing unit adjacent to a refrigerator unit. The whole roof space for these units overlooked the hotspot and study area. The boundaries for this loafing area are outlined in purple in Figure 6.4.
- Building 5: A large warehouse on the east side of the Trader's Car Park. This building had a pitched roof that overlooked the study area from the west and south aspect of the building. The boundaries of this loafing area are outlined in yellow in Figure 6.4.

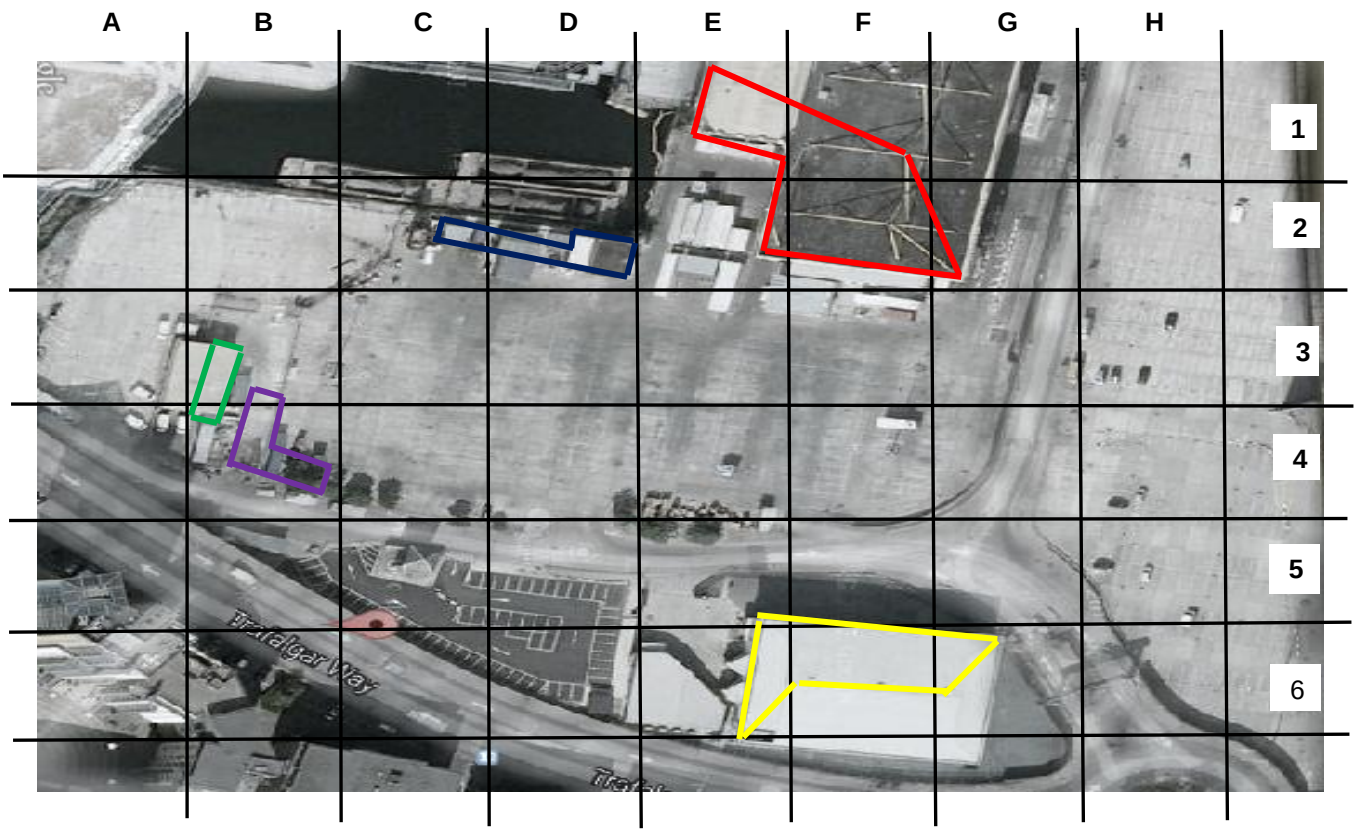


Figure 6.4. The five loafing areas at Billingsgate. Loafing areas occurred on the roofs of buildings around the main study area. The areas bounded by coloured lines represent the loafing areas of interest that overlooked the hotspot and foraging area at the study site. The five areas were: Building 1 (red); Building 2 (blue); Building 3 (green); Building 4 (purple) and Building 5 (yellow). Image taken from Google maps on 06/03/14.

To work out the mean flight distance to each of the 5 loafing areas (labelled as Buildings 1-5), measurements in metres at the ground level from the hotspot to each corner point of the demarcated loafing area were taken using the ruler tool on Google Earth Pro (©2016 Google). As each loafing area was an irregular shape the number of measurement points for each building differed (Building 1: 6 measurement points; Building 2: 12 measurement points; Building 3: 4 measurement points; Building 4: 8 measurement points; Building 5: 4 measurement points). Figure 6.5 shows an image of the study area taken from Google Earth Pro with red lines from the hotspot to each of the measurement points on the loafing Buildings. The height of the building at each point that was

measured was also calculated in metres using the elevation tool on Google Earth Pro (©2016 Google). With a ground level distance measurement and perpendicular height measurement it was then possible to calculate a line-of-sight flight distance to the hotspot from each point of measurement using the Pythagorean theorem. As the measurement points represented the boundaries of a loafing area and therefore the minimum and maximum flight distances from each loafing building to the hotspot, a single mean flight distance score was obtained for each building by taking the average of the flight distances calculated for that building. These mean flight distances are listed in Table 6.1.

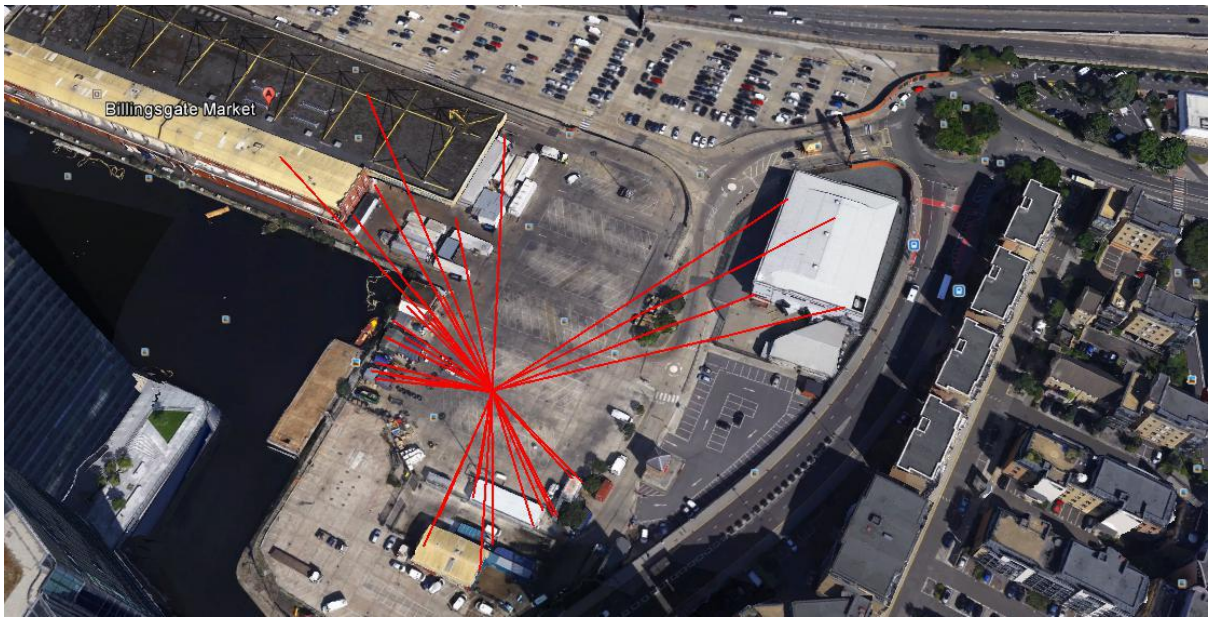


Figure 6.5. Aerial photograph of the study area highlighting in red each of the ground level measurement points from the patch hotspot in the Trader's Car Park to the loafing area boundary points on buildings 1-5. 'Billingsgate' 51°30'22.06"N 0°00'42.50"W, image taken from Google Earth Pro (©2016 Google) on 08/07/16.

Table 6.1. Mean flight distances in metres from each of the 5 loafing buildings to the hotspot for foraging patches.

Building	Mean flight distance (metres)
1	95.79
2	35.17
3	49.13
4	40.17
5	113.84

It was hypothesised that gulls would distribute themselves differently around the site whilst loafing based on whether they were subordinate or dominant birds, following the categorisation described

earlier in this chapter. It was predicted that subordinate gulls would have greater need to stay closer to the locations where food was most likely to appear, so they could get to it first and thereby gain a finder's advantage (Chapter 1 section 1.3.3) before the arrival of more dominant individuals. Based on the mean flight distances calculated for the 5 loafing buildings this led specifically to the prediction that there would be significantly more subordinates loafing on buildings 2, 3 and 4 and in contrast significantly more dominant gulls loafing on buildings 1 and 5. A Chi-square analysis was conducted to investigate whether there was a significant association between the status of gulls (dominant or subordinate) and the frequency with which they loafed on buildings based on their proximity to the patch hotspot.

6.3.4 and 6.3.5 – Part C and D: Do subordinate birds arrive at foraging patches first and are they quicker to engage in risky foraging behaviours?

A field experiment was conducted to assess the two questions for Parts C and D. This consisted of an enclosure pen, as shown in Figure 6.6, around and in which food items were provisioned. The size and calorific value of food items were known and items were located in the same positions in relation to the pen on each occasion that the field experiment was run. The pen was positioned in various places around the Trader's car park study site, with the placement being largely dictated by the space available to set up the pen on a given study day. The field experiment was conducted on 30 study days, on each day the pen was set up behaviour was recorded for one hour and then the pen was removed. If all food items were taken before the end of the hour then observations were concluded and the pen was removed.

Figure 6.6. Image of the enclosure pen used in the analysis for Parts C and D. The pen was 50cm deep and food items were provisioned in and around the pen. Latency to approach/ arrive at the pen and enter the pen to obtain food were measured for members of both subordinate and dominant status groups.

6.3.4 – Part C: Do subordinate birds arrive at foraging patches first? To address this first question, for each day of study the duration of time that it took from food being provisioned to the first individual from the two status groups to approach the pen and attempt to obtain food items was recorded. This gave a time score on each study day for each status group of latency to approach or arrive at the food patch. Times were recorded in seconds and if no member of a status group arrived at the patch before the hour of observations was concluded a maximum latency to approach score of 3600 seconds (the number of seconds in an hour) was attributed to that status group. It was predicted that subordinate gulls would be significantly more likely to be the first to arrive at food patches in order to give them a finder's advantage and opportunity to consume some food items before the arrival of dominant gulls.

The data for latency to arrive was tested for normality and homogeneity of variances. An examination of histograms of the data showed a bimodal distribution of latency times. This lack of normality was confirmed using the Shapiro-Wilk test on the complete dataset ($W=0.48$, $p<0.001$) and by assessing normality of distribution within each status group (Subordinate: $W=0.39$, $p<0.001$; Dominant: $W=0.55$, $p<0.001$). Homogeneity of variances across groups was tested using Hartley's F_{max}. This returned an F-ratio indicating that the variances of the two groups were homogenous ($F^* = 1.75 < 2.07$). Despite this finding, due to the highly significant lack of normality to the data a non-parametric statistical test was conducted. Mann-Whitney U test was used to assess differences in latency to arrive at the food patch between the two status groups.

6.3.5 – Part D: Are subordinate birds quicker to engage in more risky foraging behaviours? The enclosure pen represented a novel object that gulls had to enter in order to obtain food items provisioned inside. This required actually landing inside the pen in a relatively confined space and represented a more risky behaviour as the number of exit routes for the gull was reduced. Birds had to lift out of the pen first before flying off and the depth of the sides of the pen was 50cm. On all trials for this field experiment gulls first approached and foraged for food outside the pen. This prioritisation of food outside the pen was considered a reflection of the inherently more risky foraging behaviour required to obtain food items placed inside the pen. Entering the pen was considered a good assay of likelihood of engaging in riskier foraging behaviours. A separate analysis was therefore conducted to investigate if there was a difference between the status groups in the likelihood with which they engaged in risky foraging behaviours in order to obtain a share of the contested food items. This was assessed through the latency of individuals from the two groups to enter the pen.

Latency to enter the pen was measured in seconds and the times for the first individuals from each status group to enter the pen were recorded on each day of study. As with the previous analysis, if no individual from a status group entered the pen before the one hour time limit, that status group was given a maximum time score of 3600 seconds on that study day. It was predicted that subordinate gulls would be quicker to enter the pen as they would have to take more risks in order to acquire food in the study population where they must compete with more dominant gulls that have a higher priority of access to food than themselves.

The dataset for latency to enter the pen was tested for normality and homogeneity of variances. The data was explored graphically and showed a bimodal distribution. This non-normal distribution was confirmed with Shapiro-Wilk tests on the complete dataset for latency to enter the pen (W=0.73, p<0.001) and the data for each status group separately (Subordinate: W=0.63, p<0.001; Dominant: W=0.70, p<0.001). Hartley's F_{max} was used to test for homogeneity of variances between the groups. This showed that the variances between the groups were homogenous (F^*=1.68<2.07) for the number of trials and groups used in the analysis. The highly significant lack of normality in the distribution of the data meant that, as with the previous analysis, a non-parametric Mann Whitney U test was used to assess differences between the status groups in the latency with which they entered the pen.

6.4 – Results

6.4.1 – Part A: Is there a difference in the frequency of foraging behaviours between dominant and subordinate birds?

Table 6.2. Contingency table showing the frequencies with which different status groups occurred in the two locations at Billingsgate.

		Location		
		Building	Ground	Total
Status	Dominant	2043	513	2556
	Subordinate	1983	1791	3774
	Total	4026	2304	

Table 6.2 shows the frequency scores with which gulls in the two status groups were recorded on buildings and on the ground. A Chi-square analysis showed there was a significant association between the location of a bird and its status $X^2(1) = 493.70$, p<0.001. Cramer's V was 0.28 suggesting that about 8% of the variation in the frequencies of birds on buildings and on the ground were explained by status group. This significant difference in the status of birds between the two locations supported the first prediction made for this study. Examination of standardized residuals showed that in the dominant group significantly more birds were likely to be on buildings (z=10.4) and significantly fewer birds than expected were on the ground (z=-13.7), both of these results were significant at the p<0.001 level. Within the subordinate group standardized residuals showed that significantly fewer birds than expected were recorded on buildings (z=-8.5) and significantly more subordinate birds were on the ground (z=11.3), both of these values were significant at p<0.001. The conclusion drawn from these results is that subordinate birds spent significantly more of their time on the ground and thereby were more likely to be engaged in foraging activities than birds in the dominant group.

6.4.2 – Part B: Do subordinates loaf closer to foraging patch hotspots?

Table 6.3. Contingency table showing the frequencies with which different status groups loafed on the main buildings (1-5).

		Building					
		1	2	3	4	5	Total
Status	Dominant	497	290	171	154	683	1795
	Subordinate	186	245	581	404	419	1835
	Total	683	535	752	558	1102	

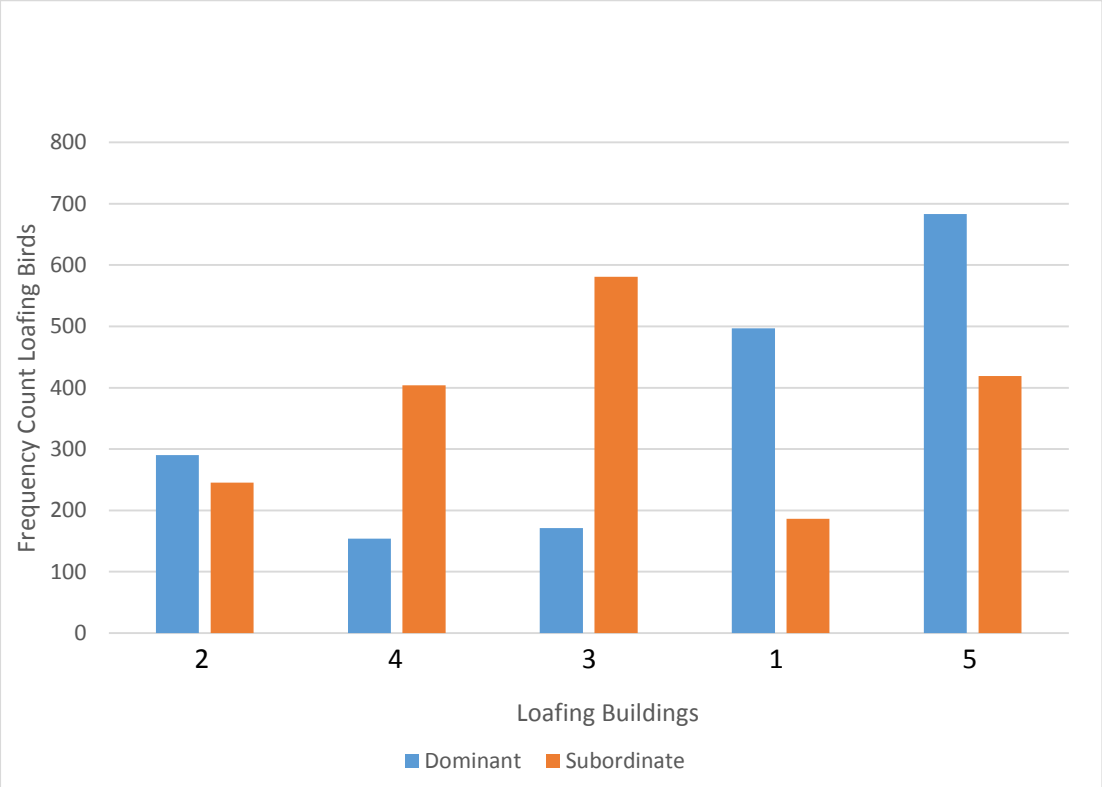


Figure 6.7. Bar chart showing distribution of dominant and subordinate birds as the distance of loafing buildings from the patch hotspot increased. The x-axis shows loafing buildings ranked from left to right in order of increasing distance from the patch hotspot.

Table 6.3 shows the frequencies with which dominant and subordinate gulls loafed on buildings 1 to 5 and Figure 6.7 depicts this information graphically with the buildings ranked in order, from left to right, with increasing mean flight distance to the hotspot. The results of the Chi-square analysis showed a highly significant association between status group and the buildings on which birds loafed. $X^2(4)=543.81$, $p<0.001$. Cramer's V was 0.39 indicating that about 15% of the variation in the frequencies of birds loafing on the 5 main buildings at the study site was explained by the status group to which the bird belonged.

Standardized residuals were examined to understand the patterns of behaviour in this significant result. These showed that there were significantly more dominant birds (z=8.7) and fewer

subordinate birds (z=-8.6) on Building 1 than would be expected by chance. This result was significant at the level p<0.001. The standardized residuals for Building 2 were non-significant (Dominant: z=1.6; Subordinate: z=-1.5) indicating that there was no difference in the frequencies with which dominant and subordinate gulls loafed on the roofs of this building. On Building 3 there were significantly more subordinate loafing gulls (z=10.3) and fewer dominant loafing gulls (z=-10.4), both of these results were highly significant at the p<0.001 level. Standardized residuals for Building 4 also showed that there were significantly more subordinate (z=7.3) and significantly fewer dominant gulls (z=-7.3) loafing at this location, again this was a highly significant result, p<0.001. The results for Building 5 showed that there were more dominant gulls (z=5.9) and fewer subordinate gulls (z=-5.8) loafing on this building than expected by chance. This result was also significant at the p<0.001 level.

It was predicted that in order to obtain a share of contested resources subordinate birds would stay closer to the areas of the study site that were the most likely locations, or hotspots, for the appearance of food patches. This meant subordinate gulls preferentially loafing on buildings 2, 3 and 4 as these were the closest loafing sites to the patch hotspot shown in Figure 6.3. In contrast, dominant gulls were predicted to have less need to stay close to resources as their status ensured them priority of access to food whenever it was available; as a consequence they were predicted to be more likely than subordinates to loaf on buildings 1 and 5 as these buildings were more distant from the foraging patch hotspot.

The results supported four of the five predictions, with subordinate gulls loafing significantly more frequently on buildings 3 and 4 and dominant gulls loafing significantly more frequently on buildings 1 and 5. The result for building 2 was the only one that did not match the prediction as no significant difference was found between the frequencies with which dominant and subordinate gulls loafed on this building. On the whole these results suggest that subordinate gulls were significantly more likely to stay closer to areas of the study site that were hotspots for the occurrence of food patches.

6.4.3 – Part C: Do subordinate birds arrive at foraging patches first? Mann-Whitney U test showed that the distribution of latency to arrive at the food patch differed significantly across the status groups (U=618.50, z=2.49, p=0.01, r=0.32). Gulls in the subordinate status group showed a much shorter latency, measured in seconds, to arrive at the pen (Mdn=147.50) and this was significantly quicker than birds in the dominant status group (Mdn=295.00). An r-value of 0.32 indicated a medium effect size for this difference, with about 10% of the variance in latency to arrive at the patch being explained by status group.

6.4.4 – Part D: Are subordinate birds quicker to engage in more risky foraging behaviours? The results of the Mann-Whitney U test showed there was a significant difference between the two status groups in their latency, measured in seconds, to enter the pen (U=697.50, z=3.75, p<0.001, r=0.48). Gulls in the subordinate status group were significantly quicker to enter the pen (Subordinate:

Mdn=315.50) than were dominant gulls (Dominant: Mdn=3600.00), suggesting that subordinate gulls were significantly quicker than dominants to engage in risky foraging behaviours when competing for a share of resources. As can be seen by the median score for dominant birds, this did not differ from the maximum score that could be attributed to each group, indicating that in many cases gulls from the dominant group did not actually enter the pen to forage for food items. The effect size for this result (r=0.48) was medium to large suggesting about 23% of the variance in latency to enter the pen was accounted for by status group.

6.5 – Discussion

This study sought to investigate the ways in which gulls at Billingsgate of lower competitive ability, that being birds of smaller size, strength and lesser foraging skill – termed subordinates, responded behaviourally to try and obtain a share of the food resources in that environment. It was hypothesized that subordinates would behave differently to dominant gulls (larger, more powerful birds and more skilled adult foragers) in a number of ways that were investigated through four analyses. The predictions made in relation to these analyses were: Part A: Subordinate gulls would spend more time foraging in order to meet their energy needs. Part B: Subordinate gulls would loaf closer to the hotspot at the site where food regularly became available. Part C: Following on from prediction B, subordinate gulls would be first to arrive at a new food patch to obtain a finder's advantage and consume some food items before being displaced by dominant gulls. Part D: Subordinates would be quicker to engage in more risky foraging behaviour. This was assessed through latency to enter a pen in order to obtain food items. The pen being a novel anthropogenic object, entering into which reduced flight options and was a potentially risky behaviour. I consider the result of each of these predictions in turn below.

6.5.2 – Part A: Subordinate gulls were significantly more likely to be on the ground than dominant gulls. This was viewed as an effective assay that subordinate gulls were much more likely to be engaged in foraging activities than dominant gulls at any given time. This meant that subordinates spent more time foraging than dominants and supported the first prediction. This extra time needed by subordinates to acquire food and meet their energy demands may have been the result of poorer foraging ability in juveniles or may have compensated for having to settle for lower-value food items due to their inability to compete directly with dominants.

The result agreed with previous research that has reported differences between adult and juvenile seabirds in the amount of their daily time budget allocated to foraging (Burger, 1980; Gochfield & Burger, 1981; Verbeek, 1977a). In many cases this difference is linked to differences in foraging skill. For example, Bertellotti and Yorio (2000) note that juvenile gulls make more handling errors than adults and this will translate into a slower intake rate and greater time needed to handle and process food items. However, the greater foraging time of subordinates may also be due to subordinates paying an interference cost from foraging alongside dominant individuals. These costs force the subordinate to adjust its foraging behaviour to compensate for its lower priority of access to resources (Rands, 2011). It is expected that both of these mechanisms influenced behaviour in the Billingsgate population.

6.5.3 – Part B: Five specific predictions were made to assess whether subordinate gulls loafed closer to the patch hotspot, thereby positioning themselves nearer to the locations where food regularly appeared. These predictions were that subordinates would loaf on buildings 2, 3 and 4 (Figure 6.4), these being the closest buildings to the hotspot, and dominants would loaf on buildings 1 and 5 (Figure 6.4) which were further away from the hotspot.

The results for buildings 3 and 4 supported the predictions, with a significantly greater number of subordinates loafing on these roofs. The results for buildings 1 and 5 also supported the predictions with a significantly greater number of dominant gulls loafing on these two buildings. The only prediction that was not supported was building 2, on which it was predicted more subordinate gulls would loaf. The result for building 2 showed no difference between subordinates and dominants in the extent to which they loafed on this roof. As building 2 was actually closest to the hotspot, with a mean flight distance of 35.17m, this seems to provide a strong contradiction of the hypothesis despite the four other supported predictions. The result for building 2 could, however, be explained by other factors. It was noted that a pair of adult HG nested to breed on the flat roofed area of building 2, this meant a constant presence of birds from the dominant status group for the part of the year covering the breeding season. As breeding gulls are very territorial and aggressive it is likely that this breeding pair chased-off and displaced subordinates that attempted to loaf on building 2. This single factor could have disrupted the expected pattern of loafing behaviour on building 2 and may account for the observed result.

The results observed for the five predictions made for the part B analysis may be plausibly explained by alternative hypotheses. For instance, there has been no specific research examining whether gulls position themselves strategically in order to optimize their food acquisition when competing in dominance stratified groups as hypothesised here. However, previous research has looked at how dominance interactions can lead to spatial displacement of subordinate individuals away from a patch or may force subordinates into riskier positions (Rands, 2011). It is possible that subordinates positioned themselves while loafing so they could get to food before dominants, but there may have been other criteria upon which loafing positions were chosen and this may have been dictated by dominant birds. This would make intuitive sense as dominants have priority of access to food resources, so there is no reason to believe they wouldn't also have first choice with other resources in the environment, such as choice of the best perching sites.

An alternative hypothesis is that loafing positions were chosen based on some other criteria such as the safety of the positions. This could be linked to multiple factors including the elevation of the loafing positions. It was noted that the buildings most strongly associated with dominants (buildings 1 and 5) were also the tallest buildings at the study site on which gulls loafed. The height of these buildings may have made them less accessible and given them a better view overlooking the surrounding area, making them safer loafing points. However, even if it is the case that dominants dictate interactions in relations to all resources in the environment this does not invalidate the original prediction that subordinates loaf closer to likely food sources.

On the whole, with four out of five predictions supported, it remains plausible that subordinates stayed closer to the patch hotspot. A stronger argument for this could be made if it was demonstrated that loafing in these locations resulted in subordinates being the first to arrive at food patches. Such an analysis was the focus of part C.

6.5.4 – Part C: Subordinate gulls were significantly more likely to be the first to arrive at food patches provisioned as part of the field experiment. This supported the prediction that subordinates would arrive first at patches as by being first to arrive they would acquire a finder's advantage (Giraldeau & Caraco, 2000), allowing them to consume some food items prior to the arrival of dominant gulls.

Previous research by Hansen (1986) studying competitive interactions between bald eagles (*Haliaeetus leucocephalus*) found similar results, with juveniles, subordinate competitors in aggregations of that species, frequently being the first to food. The results of the current study suggest that being first to arrive is also a useful strategy for subordinate gulls at Billingsgate. This provides an additional strand of support for the interpretation of the analysis that showed subordinates loaf closer to the patch hotspot (Part B) as this allows an advantage in getting to food first.

6.5.5 – Part D: Considering behaviour around food items provisioned inside the pen enclosure, subordinate gulls were significantly quicker than dominant individuals to enter the pen to obtain the food items provisioned within. This supported the prediction that subordinates would enter the pen first.

Entering the pen was a behaviour that involved the risk of getting trapped and reduced the number of escape routes. It was hypothesised that subordinates would have to engage in more risky foraging behaviours in order to compete with dominants for food at Billingsgate, this included taking risks such as foraging in areas where dominants were reluctant to go. Research on passerine species (Blue tits (*Parus caruleus*): Hegner, 1985; White-throated sparrows (*Zonotrichia albicollis*): Schneider, 1984) has demonstrated a similar difference in foraging behaviour between dominant and subordinate birds to those reported here, with subordinates being more likely to engage in risky behaviours, such as foraging further from cover than dominant birds.

It is believed that this is the first time differences in risky foraging behaviours linked to status have been demonstrated in gulls through experimental manipulation of food patches. Whether this interpretation of the result is accepted will depend in the extent to which entering the pen is viewed as a valid assay of risky behaviour. As gulls are known to be initially cautious with objects or apparatus that are novel or seem out of place (Scott, Duncan & Green, 2014) using latency to enter the pen as a measure of perceived risk seems acceptable.

A criticism that could be made of this analysis is that not all individuals across the status groups are morphologically identical so entering the trap could be considered less risky for some than others. This may particularly be the case for BHG, a species in the subordinate status group that is notably smaller than the other foraging gull species at Billingsgate. It could be argued that entering the pen is a relatively less risky behaviour for BHG as their smaller size makes it less of a confined space. However, even with this criticism taken into account the result still illustrates a key question being investigated in this study: that subordinate gulls adjust their behaviour or forage differently to dominant gulls in order to compete for a share of the resources at Billingsgate.

6.6 – Summary

The four analyses conducted for this study demonstrated that subordinate gulls foraged differently to dominants at Billingsgate. Subordinates spent more time foraging and the results indicated that they positioned themselves around the site to stay close to prominent locations for food. Further research to understand how gulls might be using space at the site including what criteria are affecting the selection of loafing locations is needed as the results for the loafing analysis (Part B) were inconclusive and could be interpreted in multiple ways. The hypothesis that subordinates stay close to where food patches regularly appear obtained some support from the result showing that subordinates arrived first at food patches (Part C). As the site is small and easy for all foragers to search, the finder's advantage subordinates gained from arriving first at food appears to be an important strategy that allows them to compete with dominants in indirect ways. Taking greater risks whilst foraging (Part D) is another way in which subordinates acquire food at Billingsgate.

A limitation of the current study may be that the dichotomy of the population into two categories of subordinate and dominant is largely artificial. There is a great deal of variation between individuals within these categories in terms of morphology and foraging behaviours. For example, juvenile HG and BHG were both categorised as subordinate but differ considerably in terms of size and will likely show different preferences in the size of prey items they will prioritise. Despite these issues, the status categorisation used was believed to be effective enough to capture something essential about the priority of access to resources that existed in the Billingsgate population.

The research described here could be developed further with a more fine-grained examination of the strategies and behaviours used by all species and ages in the population. This would provide a deeper understanding of the status interactions in the population and would give some indication of whether the status dichotomy used provides an accurate description of behavioural differences in the population at a general level. However, this would have been a lengthy and descriptive analysis beyond the aims set for this third study.

The main aim of this study was to identify the ways, beyond kleptoparasitic strategies, in which subordinate gulls competed behaviourally with dominant individuals. Four candidate strategies, with varying degrees of support, were identified as summarised in this chapter. In the next chapter I will continue to focus solely on the urban population at Billingsgate and will return to analysing the main behaviour of interest in this thesis, kleptoparasitism. In study 4 I will develop a game-theoretical model of the Billingsgate population to try and ascertain how good are the behavioural decisions being made by foragers in that population.

(7)

Chapter 7 – Study 4: A game-theoretical model of the Billingsgate foraging population

7.1 – Introduction

In previous chapters I have described the data collected on foraging and kleptoparasitic behaviours at the study sites of Billingsgate and Brancaster, conducted analyses to examine some of the main patterns of behaviour and highlighted differences in behaviour between the two sites, and looked at the ways in which subordinate foragers might compete for resources at Billingsgate. In this chapter I describe research assessing the effectiveness of the foraging decisions made by individuals in the urban study population at Billingsgate through an analysis of their use of kleptoparasitic behaviours. This was achieved using evolutionary game theory to develop a mathematical model of kleptoparasitism. The actual foraging data from Billingsgate was then compared with the results of the mathematical model to investigate what this can tell us about the optimality of kleptoparasitism as it is used by gulls foraging at Billingsgate.

7.2 – Study rationale and predictions

Previous research studies have provided empirical validation of the predictions of individual elements of kleptoparasitism models using wild populations of foragers (Hansen, 1986; Thompson, 1986; Barnard and Thompson, 1985; Morand-Ferron, Giraldeau & Lefebvre, 2007; Chapter 2, section 2.4 and 2.6). However, no study has developed a model of a wild foraging population and investigated whether the density of producers to scroungers in that population is at an equilibrium, or whether individual foragers are making good behavioural decisions by using evolutionarily stable strategies (ESS – Chapter 1, section 1.2 and Appendix B) in the correct environmental conditions. This study attempted to do that by developing a model based on the parameters and strategies available to the foraging gull population at Billingsgate. That model was then compared to the foraging behaviour recorded at Billingsgate to see how closely the foraging strategies of gulls corresponded to the ESS predictions of the model.

The Billingsgate study population forage for food waste in a car park at Billingsgate market. The Billingsgate population was the focus of this study because the population consists of three different gull species (HG: Herring gull (*Larus argentatus*), GBB: Great black-backed gull (*Larus marinus*), and BHG: Black-headed gull (*Chroicocephalus ridibundus*)) that are the only organisms that forage for food at this location. So, there are no competitor species outside the three species that make up the model system of interest that may complicate the analysis of kleptoparasitic behaviours.

The game-theoretical compartmental modelling approach developed by Broom and colleagues (Broom & Ruxton, 1998; Broom & Ruxton, 2003; Broom, Luther & Ruxton, 2004; Broom & Rychtar, 2007; Broom & Rychtar, 2009; Hadjichrysanthou & Broom, 2012; Chapter 1, section 1.3.4) was used to calculate the equilibrium density of each behaviour in the population and to conduct an analysis of whether individuals in the population are making their best behavioural responses in their use of kleptoparasitism at Billingsgate. This model of kleptoparasitism use in the gull population at Billingsgate returned equilibrium densities and ESS's in given environmental conditions that were compared and calibrated against the real data on kleptoparasitism obtained from that study site. The purpose of this being to provide insights into whether kleptoparasitism functions to allow gulls to behave adaptively in novel, or changed, environmental conditions. A behaviour that is adaptive in one environment need not be adaptive in another. If kleptoparasitism use was demonstrated to be adaptive at Billingsgate this would contribute to our understanding of kleptoparasitism as a flexible behavioural strategy.

As natural selection is expected to produce foragers that are efficient and make effective behavioural decisions, it was predicted that the density or frequency of kleptoparasites to producers at Billingsgate would be at or close to equilibrium densities predicted by the model. This is because the population is stable and the food that is available at this site is regularly scheduled, making the competitions individuals engage in iterations of very similar contests over resources. Foragers at Billingsgate are thereby expected to have converged over time on an equilibrium density of kleptoparasites to producers. Further, it was predicted that individual gulls in the foraging population would also be effective at deciding which behavioural strategy was the best (the ESS) in different environmental conditions and to adjust their behaviour accordingly as environmental parameters, such as food availability and population density, change. This was expected as kleptoparasitic strategies in wild gull populations have in previous research been shown to be facultative responses to changing environmental conditions (Maniscalco & Ostrand, 1997) and as kleptoparasitism is ubiquitous among these species, that are highly mobile and encounter varied environmental conditions, it is assumed to be a beneficial foraging strategy with significant adaptive value.

7.3 – Background

The series of compartmental kleptoparasitism models developed from Broom and Ruxton (1998) (Chapter 1, section 1.3.4) provided a suitable approach to modelling the kleptoparasitic interactions of the study population at Billingsgate and a number of features of the foraging environment at Billingsgate made it a useful candidate for using mathematical modelling as a study tool. First, as the site is an anthropogenic environment and not a complex natural food web this allowed me to consider Billingsgate as a kind of natural laboratory. The foraging area at Billingsgate is discrete and of a fixed size (the area of the Trader's car park, see Appendix D), this meant that travel time costs between patches in the foraging area could be largely discounted. In addition, the population at Billingsgate consists of three gull species all competing to exploit the same anthropogenic food discards, there are

no other trophic levels involved, no other competitor species from outside the *Laridae* family and no predator species that might affect foraging behaviour that needed to be considered. All of the above factors made it easier to meet some of the simplifying assumptions necessary when trying to model behaviour mathematically.

Second, as all three species are gull species they effectively have the same behavioural abilities and design with which to manipulate their environment when foraging, despite differing in competitive ability due to size differences. Having a standardised model forager again simplified the mathematics needed to model the foraging situation.

Third, the population at Billingsgate is stable. Birds are able to arrive and leave but on the whole the size and composition of the population exploiting food resources at the site remains the same. This stability makes the boundaries of the Billingsgate study population more clearly demarcated than is often possible for a wild population of birds. This fits with the assumption of a foraging population of fixed density used in the modelling approach of Broom and colleagues (Chapter 1, section 1.3.4).

Fourth, the real foraging data recorded at Billingsgate was obtained using observational field methods. This meant that it was not possible to directly measure the energetic costs of fighting over a food item or any possible injury costs to the individuals involved. However, the observational methods used did permit the costs of fights and searching for food items to be measured in terms of the duration of time they took, this matched the method for assessing costs used in the various models developed by Broom and colleagues.

The foraging behaviours observed at Billingsgate that were considered in this model are: searching for food items, handling food items and two kleptoparasitic strategies, aggressive kleptoparasitism and stealth kleptoparasitism (See chapter 3 section 3.4.2.1 and 3.4.2.2 for the operational definition used for these two strategies). A forager encountering a handler can choose to ignore the handler and keep searching or attack the handler using either aggressive or stealth kleptoparasitism. Similarly, a handler attacked by another forager can choose to defend or surrender its food item. These interactions effectively encapsulated the behaviours of interest present in the Billingsgate population. Although there is potentially a third type of kleptoparasitic strategy that gulls can use, ‘scramble kleptoparasitism’ (See chapter 3 section 3.4.2.3 for an operational definition), it was not included in the model due to its lack of occurrence at Billingsgate.

The model developed in the remainder of this chapter considers a population containing one species of forager. This single-species model reduced the complexity of the mathematics needed to model the foraging population and the model was compared against the averaged foraging data obtained for the whole population at Billingsgate. Although the Billingsgate population contained 3 species the assumption was made that averaging the data over the whole year of study would smooth out any asymmetries in competitive ability between individuals and species and permit the population to be viewed as a large population containing just one-species. This permitted conclusions about the optimality of behaviour to be drawn at the most general level. The model was developed and solved

through four stages where candidate ESS's and the ecological conditions in which they should occur were identified. The strategies observed at Billingsgate were then compared to the model predictions as described in the results section presented later in this chapter.

7.4 – The model

Broom, Luther and Ruxton (2004) considered a population of foragers that can either attack or ignore handlers and defend or surrender food items. The model developed here extends this by considering two types of kleptoparasitic strategy and, as appropriate, I retain and extend the notation and parameters used in Broom et al. (2004) where necessary. The foraging population consists of a population density of P individuals. That foraging population (P) consists of groups of individuals in different behavioural states or compartments. A forager can only be engaged in one behavioural state and thereby can only be in one compartment at a time. At any time a proportion of the foraging population are searching (S) for food items and a proportion are handling (H) a food item. A constant density f of food items is available and a forager can search the foraging area at a rate v_f for food items. The rate at which food items are discovered is therefore $v_f f$. Similarly, the rate at which a forager can search the foraging area for handlers is v_h, so the rate at which searchers encounter handlers of food items is $v_h H$. Following Broom et al. (2004), the time that food items take to handle is modelled using an exponential probability distribution with mean t_h. Additionally, a proportion of the foraging population are engaged in fights over food items, either as kleptoparasites trying to steal an item or handlers trying to keep hold of that food item. As stated previously, two kleptoparasitic strategies are possible within this population: aggressive kleptoparasitism or stealth kleptoparasitism. At any given time a proportion of the foraging population (P) will be attempting to steal items using aggressive kleptoparasitism (A) and a proportion of handlers will be fighting against those kleptoparasites by trying to defend (D) their food item from being stolen. Likewise, a proportion of the foraging population will be attempting to steal using stealth kleptoparasitism (C) and an equal proportion of handlers will be fighting to resist (R) their food item being stolen by stealth kleptoparasites. Defending and resisting are terms that both describe the defensive behaviour of handlers that are under attack, separate terms were used, for defending against aggressive kleptoparasitism and resisting against stealth kleptoparasitism, to differentiate the two behaviours as the probability of defensive behaviour against one type of kleptoparasitism might differ from that of the other type. Defenders (D) and Resistors (R) are therefore separate behavioural states in the foraging population (P). The composition of the total foraging population by compartments that capture the different behavioural states is described by equation (1).

$$P = S + H + A + D + C + R \qquad (1)$$

Once a searcher encounters a handler it either attacks the handler using aggressive kleptoparasitism, it does this with probability p_1, or it attacks the handler using stealth kleptoparasitism, this occurs with probability p_2, otherwise it ignores the handler and continues searching for undiscovered food items, this occurs with probability $1 - p_1 - p_2$. Conversely, a handler that is found and attacked with aggressive kleptoparasitism can either defend against the attack, which it does with probability p_3, or surrender the food item without a fight, which occurs with probability $1 - p_3$. Likewise, a handler that is attacked by a searcher using stealth kleptoparasitism resists the attack with probability p_4 or surrenders the food item without a fight with probability $1 - p_4$. If a searcher attacks using aggressive or stealth kleptoparasitism and the handler defends or resists then a fight occurs. The fight lasts for a time duration that is modelled using an exponential probability distribution. In the case of aggressive kleptoparasitism the duration of the fight is drawn from an exponential distribution with mean $t_a/2$, the attacker wins the fight with probability α and the defender wins the fight with probability $1 - \alpha$. The duration of a stealth kleptoparasitism fight is also drawn from an exponential distribution with mean $t_c/2$. The stealth attacker wins the fight with probability β and the resistor wins the fight with probability $1 - \beta$. The mean duration of stealth and aggressive fights differs as a stealth fight involves less of an interaction between attacker and handler than an aggressive fight so on average $t_c < t_a$. At the end of a fight of either type the winner begins handling the contested food item and the loser resumes searching, either for food items or other handlers. The notation used for the strategies and parameters described above is summarised in Table 7.1.

In the following sections I outline the four stages through which the model was developed:

1. I describe a system of differential equations used to identify the equilibrium densities of each behavioural compartment in the population.

2. I take a focal individual perspective to outline the optimal conditions when it is advantageous for a searcher to attempt either aggressive or stealth kleptoparasitism, and outline the conditions when it is advantageous for a handler to defend or resist attempts to steal its food. These conditions are considered against various background population strategies, such as whether the rest of the population defends or surrenders food items when challenged.

3. I describe the candidate ESS strategies that may exist in the population by combining the conditions specified in stage 2 in various ways.

4. I simulate the behaviour of the foraging population at different values of the model parameters to identify which strategies are ESS's in different ecological conditions.

Then I compare the real foraging data recorded at Billingsgate with the model predictions by inputting parameters into the model that match the Billingsgate population to see if the density of different compartments in the population are close to the equilibrium densities at plausible parameter values and by assessing whether the foraging strategies of individuals that were observed in patches with

different ecological conditions at Billingsgate match the ESS strategies predicted by the model for those conditions.

Table 7.1. Model notation.

Population Densities	Definition
P	Density of the total foraging population
S	Density of searchers
H	Density of handlers
A	Density of aggressive kleptoparasites
D	Density of defenders against aggressive kleptoparasitism
C	Density of stealth kleptoparasites
R	Density of resistors against stealth kleptoparasitism
Model Parameters	
$v_f f$	Rate at which foragers find food items
$v_h H$	Rate at which searchers encounter handlers
t_h	Expected time needed for a handler to consume a food item
$t_a/2$	Expected duration of an aggressive fight
$t_c/2$	Expected duration of a stealth fight
α	Probability that the attacker wins an aggressive fight
β	Probability that the attacker wins a stealth fight
x	Avg. proportion of a food item obtained using strategy p_2
Strategies	
p_1	Probability that a searcher attacks using aggressive kleptoparasitism upon encountering a handler
p_2	Probability that a searcher attacks using stealth kleptoparasitism upon encountering a handler
p_3	Probability that a handler attacked using aggressive kleptoparasitism defends its food item
p_4	Probability that a handler attacked using stealth kleptoparasitism resists the attack for its food item

7.4.2: Stage 1: Equilibrium densities of the behavioural compartments:

If the foraging population described in the previous section and encapsulated in equation (1) is assumed to consist of only one species then the dynamics of that population are captured by the compartmental model outlined in Figure 7.1.

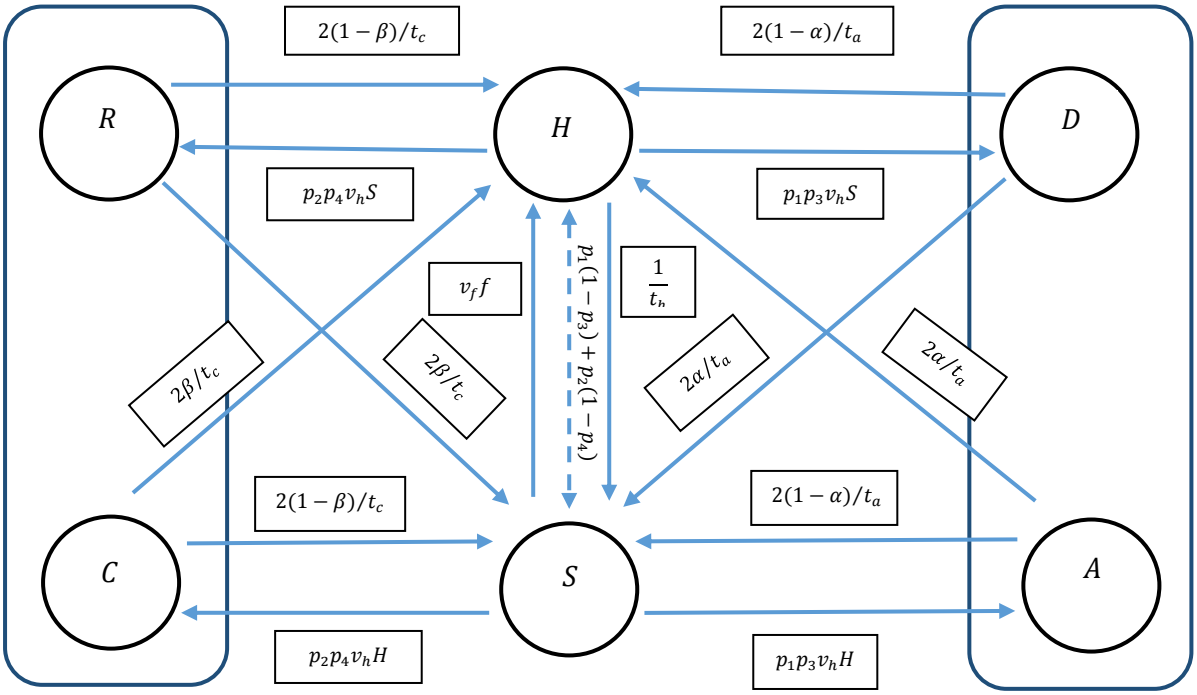


Figure 7.1. Flow diagram showing the dynamics of the Billingsgate foraging population for the single-species model. The arrows show the inflows and outflows of the different behavioural compartments and the rates at which these occur are shown along the arrows. Dashed arrows show the rates at which challenged handlers surrender food items without a fight and thereby change compartments with searchers.

To illustrate the movement of foragers through the different behavioural compartments in Figure 7.1, consider a forager that arrives at a food patch, that forager is at first a searcher (behavioural compartment S), if it finds a food item it moves to being a handler (behavioural compartment H) and this transition occurs at the rate $v_f f$. If it is then attacked by another forager trying to steal its food using a stealth kleptoparasitic strategy and the handler resists the attack it moves to behavioural compartment R where it is a resistor of stealth kleptoparasitism, this occurs at rate $p_2p_4v_hS$. Concurrently the forager that has challenged it becomes a stealth attacker and moves to behavioural compartment C at rate $p_2p_4v_hH$. If the handler wins the fight it returns to the handling compartment (H) at rate $2(1-\beta)t_c$ and the challenger returns to being a searcher (behavioural compartment S), this occurs at the same rate $2(1-\beta)t_c$.

The change in the density of each behavioural compartment as described by the rates of inflow and outflow along the arrows shown in Figure 7.1, within the closed system defined by equation (1), is described by the following system of 6 differential equations (2-7):

$$\frac{dS}{dt} = \frac{1}{t_h}H + \frac{2}{t_c}(1-\beta)C + \frac{2}{t_c}\beta R + \frac{2}{t_a}(1-\alpha)A + \frac{2}{t_a}\alpha D - v_f f S - p_1 p_3 v_h S H - p_2 p_4 v_h S H \quad (2)$$

$$\frac{dH}{dt} = v_f f S + \frac{2}{t_c}\beta C + \frac{2}{t_c}(1-\beta)R + \frac{2}{t_a}\alpha A + \frac{2}{t_a}(1-\alpha)D - \frac{1}{t_h}H - p_1 p_3 v_h S H - p_2 p_4 v_h S H \quad (3)$$

$$\frac{dC}{dt} = p_2 p_4 v_h S H - \frac{2}{t_c}C \quad (4)$$

$$\frac{dR}{dt} = p_2 p_4 v_h S H - \frac{2}{t_c}R \quad (5)$$

$$\frac{dA}{dt} = p_1 p_3 v_h S H - \frac{2}{t_a}A \quad (6)$$

$$\frac{dD}{dt} = p_1 p_3 v_h S H - \frac{2}{t_a}D \quad (7)$$

The foraging population under consideration is assumed to converge over time towards the equilibrium state (Luther & Broom (2004) provide a proof of why such an assumption is justified), this is the point at which the number of individuals in the different behavioural compartments is not changing and is found by setting each of equations 2 to 7 equal to zero and solving. So, the behavioural compartments in the population are at equilibrium densities when:

$$\frac{dS}{dt} = \frac{dH}{dt} = \frac{dC}{dt} = \frac{dR}{dt} = \frac{dA}{dt} = \frac{dD}{dt} = 0 \quad (8)$$

Solving first for the equilibrium densities of C,R, A and D (equations 4-7). From equation 4, the number of stealth kleptoparasites (C) in the population at equilibrium is given by equation 10:

$$\frac{dC}{dt} = p_2 p_4 v_h SH - \frac{2}{t_c} C = 0 \quad (9)$$

$$C = \frac{p_2 p_4 t_c v_h SH}{2} \quad (10)$$

As each fight requires a pair of individuals, it follows that the density of resistors (R) in the population at equilibrium is equal to that of stealth kleptoparasites, so R is equal to C as shown in equation 12.

$$\frac{dR}{dt} = p_2 p_4 v_h SH - \frac{2}{t_c} R = 0 \quad (11)$$

$$R = \frac{p_2 p_4 t_c v_h SH}{2} \quad (12)$$

Similarly the density of aggressive kleptoparasites (A) in the population at equilibrium is obtained by setting equation 6 equal to zero, as shown in equation 13, and solving to give equation 14.

$$\frac{dA}{dt} = p_1 p_3 v_h SH - \frac{2}{t_a} A = 0 \quad (13)$$

$$A = \frac{p_1 p_3 t_a v_h SH}{2} \quad (14)$$

Following a similar argument to that given above the density of defenders (D) is identical to the density of aggressive kleptoparasites, so at equilibrium A equals D as shown in equation 16.

$$\frac{dD}{dt} = p_1 p_3 v_h SH - \frac{2}{t_a} D = 0 \quad (15)$$

$$D = \frac{p_1 p_3 t_a v_h SH}{2} \quad (16)$$

The solutions to C,R, A and D, equations 10, 12,14 and 16, were then substituted into equation 2 which was set equal to zero (17) to give the equilibrium density of searchers (S), this solves to give equation 18.

$$\frac{dS}{dt} = \frac{1}{t_h}H + \frac{2}{t_c}(1-\beta)C + \frac{2}{t_c}\beta R + \frac{2}{t_a}(1-\alpha)A + \frac{2}{t_a}\alpha D - v_f f S - p_1 p_3 v_h S H - p_2 p_4 v_h S H = 0 \quad (17)$$

$$S = \frac{H}{t_h v_f f} \quad (18)$$

Equation 18 can then be substituted for S into equations 10, 12, 14 and 16 to give equilibrium solutions for four other behavioural compartments (C,R, A and D) specified in terms of only one unknown variable H, the density of handlers (Note that S is already explicit in terms of H). These solutions are given in equations 19, 20, 21 and 22.

$$C = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} \quad (19)$$

$$R = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} \quad (20)$$

$$A = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \quad (21)$$

$$D = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \quad (22)$$

To find the equilibrium density of handlers, the five equilibrium solution (18-22) can then be substituted into equation 1 giving equation 23, which simplifies to equation 24.

$$P = \frac{H}{t_h v_f f} + H + \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \quad (23)$$

$$P = \frac{H}{t_h v_f f} + H + \frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \quad (24)$$

Equation 24 can be solved for H to give quadratic equation 25, and the equilibrium density of handlers is the positive solution to equation 25 depicted using the quadratic formula in equation 26.

$$-(p_1 p_3 t_a + p_2 p_4 t_c) v_h H^2 - (1 + t_h v_f f) H + t_h v_f f P = 0 \quad (25)$$

$$\frac{1 + t_h v_f f \pm \sqrt{(1 + t_h v_f f)^2 - 4 \times -(p_1 p_3 t_a + p_2 p_4 t_c) v_h \times t_h v_f f P}}{2 \times -(p_1 p_3 t_a + p_2 p_4 t_c) v_h} = H \quad (26)$$

Appendix I (Section I.1) gives detailed solutions for the dynamical system of equations described in this section.

7.4.3: Stage 2: Conditions for using kleptoparasitism and defending/resisting against kleptoparasitic attacks:

In this section I outline the conditions when it is advantageous for an individual forager to attempt kleptoparasitism upon encountering a handler or to defend/resist against kleptoparasitism when that forager is a handler that has just been challenged. The two types of kleptoparasitism, aggressive and Stealth (abbreviated to AGG and ST for convenience in the following sections), have been considered separately, so the forager is assumed to use just one of these strategies and either always uses AGG or always uses ST.

Some additional assumptions of the model are introduced here. The payoffs obtained from a fight are measured in terms of units of a food item. The assumption is made that if a forager attacks using AGG and wins the fight it obtains the whole of the food item contested, so the gain obtained is the probability of winning times the value of the item, which is 1 (representing one whole food item). Likewise if the handler defends the item and wins an AGG fight it retains the whole item. It also follows that if a searcher attacks AGG and the handler surrenders, the attacker obtains the whole food item without a fight. So the gain for winning an AGG fight is $1 \times \alpha = \alpha$ (where α is the probability of the attacker winning the fight as defined in Table 7.1).

In contrast, if a forager attacks using ST and wins the assumption is made that it obtains only a portion of the food item contested if the handler defends, and the handler retains the remaining portion. This assumption exists because this strategy is a sneaky strategy that involved less of an interaction between forager and handler but often resulted in the attacker obtaining only a portion (x) of the food item (See Table 7.1). So the gain for the attacker from winning a stealth fight is $x \times \beta = \beta x$, where x is some portion less than 1, and the proportion retained by the resisting handler even if it loses is: $\beta(1 - x)$. If the forager attacks ST and loses then the handler retains the whole of the food item, and similarly if the forager attacks ST and the handler surrenders then the forager obtains the whole food item which in both cases is $1 \times \beta = \beta$.

The value of food items was measured in the way described above because the field data for real foraging behaviour at Billingsgate was collected using observational methods, so there was no way to directly measure the calorific value of different food items. The sizes of items in the environment also could not be controlled by the researcher. This limitation of the observational field methods meant that differences in the size and value of food items could not be accurately quantified but the method described above reduced the need to know these dimensions by assessing contested items as one unit of food that was either wholly or partly obtained.

In effect food items could be repeatedly stolen on multiple occasions, this requires some clarification of how potentially smaller and smaller items of food that have experienced some handling were treated, particularly in relation to ST kleptoparasitism where only portions of the food item are obtained on average. The assumption made in the model is that an item of food has the value of one whole food item regardless of whether it has previously been stolen or been part of a larger item of food. If a forager sees fit to challenge for the item then it is treated as one unit of food. It will be noted that this is akin to assuming that food items cannot be stolen multiple times and are only subject to one kleptoparasitic attempt, after which they are immediately consumed by the kleptoparasite or handler. The validity of this assumption was investigated by comparing the simplest cases possible in the population involving partial food items: whether a handler should resist against ST when attacked by a mutant kleptoparasite in a population that does not use kleptoparasitism. It was found that the conditions when it was optimal to resist were the same regardless of whether the kleptoparasitic incident was the first attempt or a subsequent attempt to steal the food. This indicated that it was valid to treat each food item as one unit of food regardless of previous handling or whether it had been subject to previous kleptoparasitic attempts. The calculations that justify this assumption are outlined in Appendix J.

A further assumption of this model, as mentioned in the previous section (See section 7.3), is that the duration of an AGG fight $(t_a/2)$ is on average longer than the duration of a ST fight $(t_c/2)$. So, an ST fight is less protracted and has a lower time cost but results in a lower payoff in terms of the portion of the food item gained on average by the attacker. This makes ST a less risky and less timely costly strategy but one with a lower payoff than AGG when both strategies are successful.

The behavioural strategies being used by the population as a whole need to be considered when trying to identify when it is advantageous for a searcher to use kleptoparasitism or for a handler to defend/ resist against kleptoparasitic attacks. In the population being modelled here the various population dynamics that are possible result in twelve situations that need to be considered to identify advantageous conditions for searchers to attack and handlers to defend/ resist.

7.4.3.2: Searchers:

Following Broom and Ruxton (1998) and Broom et al. (2004), to assess when it is advantageous for a searcher to attack a handler it is sufficient to consider the instantaneous rate at which a searcher becomes a handler after encountering a handler. When a searcher encounters a handler it must decide whether to ignore the handler and continue searching for food items or attack the handler using either AGG or ST. The strategy it should use is the one that minimises the amount of time until it becomes the handler of a food item. This is the strategy that maximises the forager's rate of gain per time foraging. If it ignores the handler then it is just a searcher and has a rate of gain of $v_f f$; if it attacks it has a rate of gain that is influenced by the time costs of the fight and if it loses the rate at which it finds other food items or handlers to challenge. The rates at which other food items or handlers are found and challenged by foragers are given by the foraging pathways T_s for AGG

attackers and T_s^* for ST attackers. These pathways are depicted in Figures 7.2 and 7.3 below. In this model the following situations need to be considered when a searcher encounters a handler:

When it is advantageous to attack, when the population resists/defends against attacks.

1. When to use AGG (handler defends & population defends).
2. When to use ST (handler resists & population resists).

When it is advantageous not to attack the handler:

3. When to ignore the handler and continue searching for food (population defends/ resists).

When to attack if the population does not resist/defend against attacks.

4. Searcher should always attack and the kleptoparasitic strategy used does not matter as both AGG and ST have the same payoff when the population surrenders. Both strategies obtain 1 whole food item.

7.4.3.3: Handlers:

When a handler is discovered by a searcher and attacked it can choose either to resist/defend the food item it is handling or can surrender the item and resume searching for a new food item. The strategy it should use is the one that minimises the amount of time until it resumes handling a food item. If it resists/ defends the food item the time to resume handling is influenced by the duration of the fight and if it loses the rate at which it encounters other food items or handlers to challenge, as stated above this search path is denoted by $T_s \; or \; T_s^*$ (Figures 7.2 and 7.3), which shows the time to acquire a food item from the start of searching. Likewise if it surrenders the food item it becomes a searcher again and resumes handling at the rate at which it finds a new food item or encounters another handler and successfully challenges them, again $T_s \; or \; T_s^*$. The following situations need to be considered when a handler is discovered by a searcher:

When it is advantageous for a handler to resist/defend in a population where searchers attack and the rest of the handling population resists/defends:

5. When to defend against AGG (population defends and handler's searching strategy is AGG).
6. When to defend against AGG (population defends and handler's searching strategy is ST).
7. When to resist against ST (population resists and handler's searching strategy is ST).
8. When to resist against ST (population resists and handler's searching strategy is AGG).

When it is advantageous for a handler to resist/defend in a population where searchers attack and the rest of the handling population does not resist:

9. When to defend against AGG (population surrenders).
10. When to resist against ST (population surrenders).

(In these two cases the handler's searching pathways $(T_s or\ T_s^*)$ are identical as the payoff for both AGG and ST is equal when the population surrenders food items. $T_s\ and\ T_s^*$ simplify to T_s^+ given by equation (37)).

When it is advantageous for a handler to resist/defend in a population where searchers do not attack but the forager is attacked by a mutant challenger:

11. When to defend AGG against a mutant AGG challenger.
12. When to resist ST against a mutant ST challenger.
    (In these two cases the handler's searching pathways $(T_s or\ T_s^*)$ are identical as the population does not attack, so all individuals acquire food at the rate $v_f f$. The simplification of $T_s\ and\ T_s^*$ to this rate is given by T_s' in equation (42)).

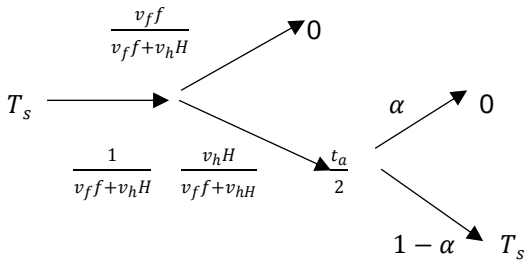


Figure 7.2. Searching pathway for an AGG forager. T_s is the time required, from the start of searching, to either find a food item or successfully steal from another handler using AGG. Zero (0) indicates the searcher successfully acquires food and exits the searching pathway.

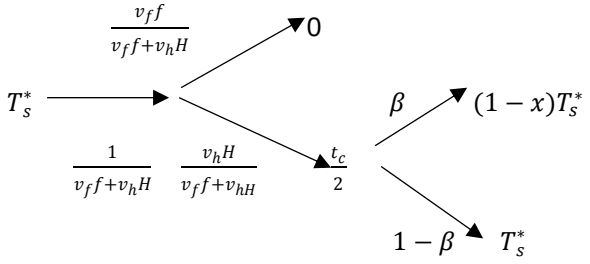


Figure 7.3. Searching pathway for an ST forager. T_s^* is the time required from the start of searching to either find a new food item or successfully steal from another handler using ST. Zero (0) indicates the searcher successfully finds food and exits the searching pathway. When successful in using ST the forager still has only acquired a portion x of a food item and still has a search time of $(1-x)T_s^*$ before it obtains food to the value of a whole food item.

Working through situations 1-12 outlined above in turn results in 12 conditions for a forager's behaviour to be advantageous in the situations described.

7.4.3.4: Searcher:

Situations 1, 2 and 3 (Section 7.4.3.2). When to attack AGG, ST or ignore the handler (handler defends/ resists & the population defends/ resists)

Considering first situations 1 to 3, the strategy of a searcher in a population that defends/ resists kleptoparasitic attacks. The searcher has three possible strategies when it encounters a handler in such a population and these equate to situations 1 to 3 described above, the searcher can either attack AGG, attack ST, or ignore the handler and continue searching for food. The strategy it should use is the one that gives it the largest payoff. Only one of these strategies can be the best strategy at any one time and to know which one this is we must first consider what the rate of gain is for each strategy.

Rate of gain from attacking AGG (Handler defends & Population defends):

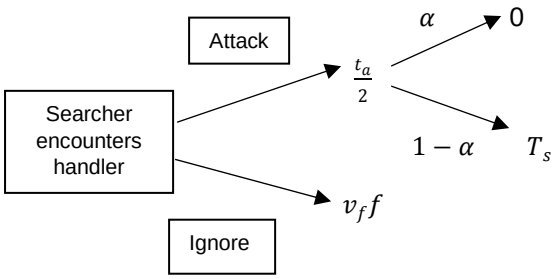


Figure 7.4. Phase diagram showing the decision points for an AGG searcher that has just encountered a handler. T_s indicates that the searcher returns to the start of that search pathway and 0 indicates that the searcher obtains the food item and successfully exits the search.

Following Figure 7.4, if an AGG attacker challenges it experiences a time cost $t_a/2$ and if it loses the fight it returns to searching and follows path T_s as shown in Figure 7.2. The pathway T_s is captured in the formula given in equation 27 which can be simplified into equation 28.

$$T_s = \frac{1}{v_f f + v_h H} + \left(\frac{v_h H}{v_f f + v_h H}\right)\left(\frac{t_a}{2} + (1-\alpha)T_s\right) \quad (27)$$

$$T_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} \quad (28)$$

Combining the foraging decision tree and foraging pathways from Figures 7.2 and 7.4, the rate of gain for a searcher that attacks handlers using the AGG strategy, in a population that defends, is given by inequality 29.

$$\frac{t_a}{2} + (1-\propto)T_s < \frac{1}{v_f f} \tag{29}$$

Rate of gain from attacking ST (Handler resists and Population resists):

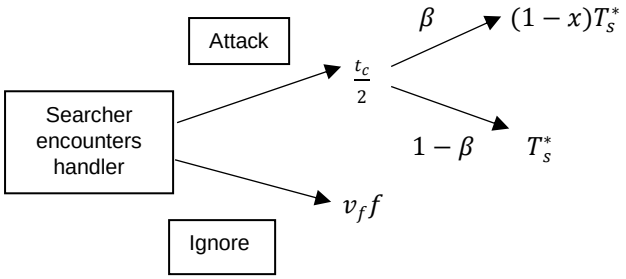


Figure 7.5. Phase diagram showing the decision points for a ST searcher that has just encountered a handler. T_s^* indicates that the searcher returns to the start of that search pathway and $(1-x)T_s^*$ indicates that as the proportion of a whole food item the attacker obtains by winning (βx) is less than one whole food item it does not exit but follows search pathway T_s^* one more time to try and obtain the remaining food value up to one food item $(1-x)$.

Following Figure 7.5 if an ST attacker challenges it incurs a fight time cost of $t_c/2$ and if it loses it follows the search pathway T_s^* shown in Figure 7.3. T_s^* is captured in formula 30.

$$T_s^* = \frac{1}{v_f f + v_h H} + \left(\frac{v_h H}{v_f f + v_h H}\right)\left(\frac{t_c}{2} + (1-\beta)T_s^* + (1-x)T_s^*\right) \tag{30}$$

Combining the foraging decisions and pathways from Figures 7.3 and 7.5, a searcher that uses ST has a rate of gain given by inequality 31.

$$\frac{t_c}{2} + (1-\beta)T_s^* + \beta(1-x)T_s^* < \frac{1}{v_f f} \tag{31}$$

(Note: The factor x in the above formula represents the proportion of the food item obtained by the ST strategy which on average is <1).

Rate of gain from ignoring the handler and continuing to search for food items (Population defends/ resists):

If the searcher chooses not to attack, ignores the handler and continues searching for food items its rate of gain is simply the rate at which it finds food, which in this population is given by the expression shown in 32.

$$v_f f \qquad (32)$$

Conditions when each strategy results in the highest rate of gain (Situations 1, 2 and 3):

Knowing the rates of gain for each of the three possible strategies a searcher can use, given by the expressions in formulas 29, 31, and 32, it is possible to specify the conditions under which each behaviour is the best strategy to take. These are given by A1a, A1b, and A1c.

1. When to attack AGG:

The condition for AGG to be advantageous occurs when the searcher becomes a handler more quickly by attacking AGG than by attacking ST or continuing to search for a food item. This produces its highest rate of food intake. A searcher should attack AGG (in a situation where the handler defends & population defends) when its rate of gain meets the condition in A1a:

$$\boldsymbol{\frac{2\alpha}{t_a} > max\left(\frac{2\beta x}{t_c}, v_f f\right)} \qquad (\boldsymbol{A1a})$$

2. When to attack ST:

The condition for ST to be advantageous occurs when the searcher becomes a handler more quickly by attacking ST than by attacking AGG or continuing to search for a food item. A searcher should attack ST (in a situation where the handler resists & population resists) when its rate of gain satisfies the conditions in A1b:

$$\boldsymbol{\frac{2\beta x}{t_c} > max\left(\frac{2\alpha}{t_a}, v_f f\right)} \qquad (\boldsymbol{A1b})$$

3. When to ignore the handler:

In a population that defends and resists kleptoparasitic attacks the searcher should ignore handlers and continue to search for food when $v_f f$ is greater than the expressions specified in conditions A1a and A1b, as below in inequality A1c:

$$\boldsymbol{v_f f > max\left(\frac{2\alpha}{t_a}, \frac{2\beta x}{t_c}\right)} \qquad (\boldsymbol{A1c})$$

4. When to attack AGG or ST (handler surrenders and the population surrender food items)

In the situation where a searcher has just encountered a handler and the handler will surrender if attacked the quickest way to become a handler is to always attack. Which kleptoparasitic strategy the searcher will use is dependent on what strategies the searcher is capable of using against the handler. In the case where the searcher is capable of using both strategies either strategy that is used will result in the same payoff. So, if the handler will surrender, which strategy is used is of no consequence. If the searcher attacks AGG and the handler surrenders the searcher obtains 1 whole unit of food. If the searcher attacks stealth and the handler surrenders the searcher again obtains 1 whole unit of food. In this situation the payoff for AGG is α, the payoff for ST is β and $\alpha = \beta = 1$. It can be concluded from this that if the handler surrenders the searcher should either always attack AGG or always attack ST.

Upon encountering a handler, a searcher should attack (AGG or ST) in a situation where the handler surrenders when the condition in A2 is met. In a population that always surrenders A2 will always hold and the searcher should always attack.

$$\boldsymbol{\infty > v_f f} \qquad (\boldsymbol{A2})$$

7.4.3.5: Handler:

Situations 5&6. When to defend against AGG (population defends)

In this situation a handler is found by a searcher and attacked AGG. Under what conditions should the handler defend the food item? The conditions are going to differ slightly depending on the behaviour of the handler when it becomes a searcher. Just because the handler has been challenged using AGG does not necessarily mean that the handler is a forager that uses AGG when it is a searcher. The two possible paths for a handler that is attacked AGG depend on whether it is an ST or AGG

attacker when foraging, this will be reflected in its foraging paths T_s or T_s^* as depicted in the two phase diagrams shown in Figures 7.6 and 7.7.

5. Defend against AGG (handler is an AGG kleptoparasite when it reverts to searching)

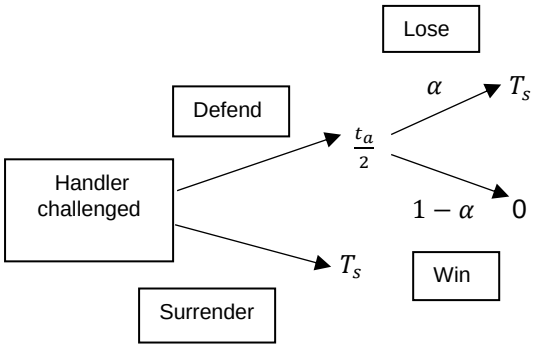


Figure 7.6. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked AGG. T_s denotes that the handler is itself a user of the AGG strategy when it returns to searching.

T_s is again given by the formula shown in equation 28. As we are now considering the interaction from the perspective of a handler, the probability that a handler loses is α (the same probability the attacker wins), so, the conditions for Defend to be advantageous (the handler resumes handling more quickly) are given by inequality 33.

$$\frac{t_a}{2} + \alpha T_s < T_s \qquad (33)$$

This can be simplified to give:

$$\boldsymbol{v_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)v_h H} \qquad (\boldsymbol{A3})$$

6. Defend against AGG (handler is an ST kleptoparasite when it reverts to searching)

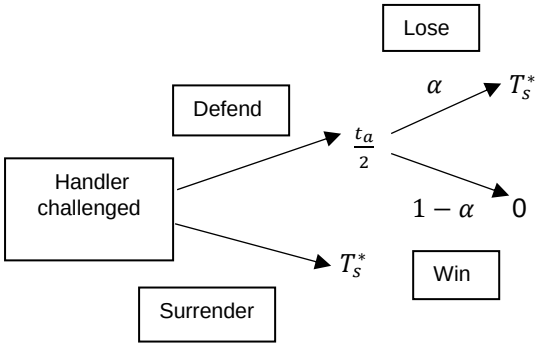


Figure 7.7. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked AGG. T_s^* denotes that the handler is a user of the ST strategy when it returns to searching.

The foraging pathway shown in the above phase diagram is almost identical to Figure 7.6 except if the handler loses the AGG fight and resumes searching, because it is a ST kleptoparasite, its search path is now T_s^* which from previous arguments is given by equation 30.

In this case, the conditions for Defend to be advantageous (the handler resumes handling more quickly) are specified in inequality 34.

$$\frac{t_a}{2} + \alpha T_s^* < T_s^* \qquad (34)$$

This can be simplified to give:

$$\boldsymbol{v_f f < \frac{(1-\alpha)(2+v_h t_c H)}{t_a} - \beta v_h H} \qquad (\boldsymbol{A4})$$

Situations 7 & 8. When to resist ST (population resists)

In this situation the handler is found by a searcher and attacked ST. Under what conditions should it resist the ST attack? As with the foraging situations outlined in situations 5 and 6 the conditions are going to differ depending on whether the handler, when it resumes foraging, is an AGG or ST kleptoparasite.

7. Resist against ST (handler is an ST kleptoparasite when it reverts to searching)

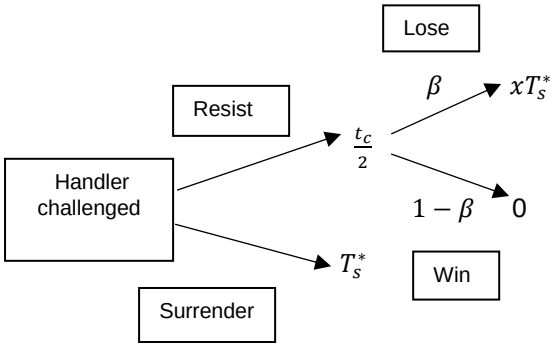


Figure 7.8. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked ST. T_s^* denotes that the handler is a user of the ST strategy when it resumes searching.

The handler is challenged ST and if it resists the attack it incurs a time cost of $t_c/2$ and if it loses, which happens with probability β, it must resume searching and follows the search path T_s^* shown in Figure 7.3 and equation 30. The leads to the conditions for resist to be advantageous (the handler resumes handling more quickly), in a population that resists, when the inequality in 35 is satisfied.

$$\frac{t_c}{2} + \beta x T_s^* < T_s^* \qquad (35)$$

This can be simplified to give A5. Note that the factor of $1 - \beta x$ represents the proportion of the food item that a handler retains even if it resists stealth and loses.

$$\boldsymbol{v_f f < \frac{2(1-\beta x)}{t_c} + (1-\beta-\beta x) v_h H} \qquad \boldsymbol{(A5)}$$

8. Resist against ST (handler is an AGG kleptoparasite when it reverts to searching)

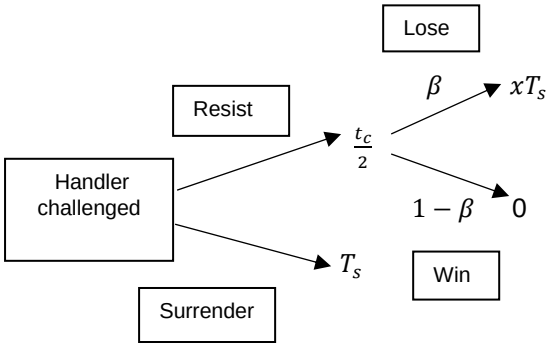


Figure 7.9. Phase diagram showing the decision faced by a handler that is found by a searcher and attacked ST. T_s denotes that the handler is a user of the AGG strategy when it resumes searching.

On this occasion the handler is challenged stealth and if it resists it incurs the time cost of a stealth fight $(t_c/2)$ and if it loses follows search pathway T_s as it is an AGG attacker when it encounters other handlers. T_s, as stated previously, is the search pathway in Figure 7.2 and equation 28. The conditions for resist to be advantageous (the handler resumes handling more quickly) are therefore described by 36.

$$\frac{t_c}{2} + \beta x T_s < T_s \qquad (36)$$

This gives condition A6.

$$\boldsymbol{v_f f < \frac{(1-\beta x)(2+v_h t_a H)}{t_c} - \alpha v_h H} \qquad \boldsymbol{(A6)}$$

Situations 9 & 10. When to resist/defend when the population surrenders food items

In the situation where the population does not resist or defend food items but surrenders them straight away the time to acquire a food item and become a handler from the start of searching (T_s for AGG kleptoparasites and T_s^* for ST kleptoparasites) simplifies to the same expression for both AGG and ST foragers denoted by T_s^+, this is the rate at which a searcher encounters food or a handler:

$$T_s^+ = \frac{1}{v_f f + v_h H} \tag{37}$$

9. Defend against AGG (population surrenders)

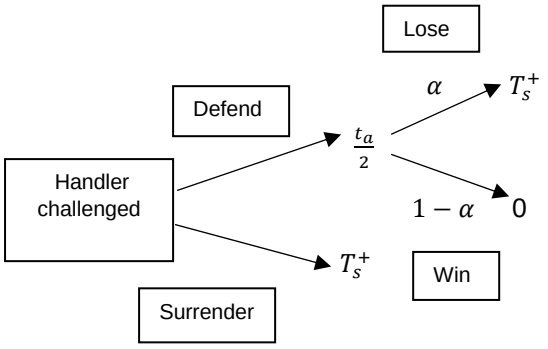


Figure 7.10. Phase diagram showing the decision points for handler that is challenged AGG in a population that surrenders food items.

The conditions for Defend to be advantageous in a population where all foragers surrender food items when challenged are given by 38 and 39.

$$\frac{t_a}{2} + \alpha T_s^+ < T_s^+ \tag{38}$$

$$\frac{t_a}{2} + \alpha\left(\frac{1}{v_f f + v_h H}\right) < \frac{1}{v_f f + v_h H} \tag{39}$$

Inequality 39 simplifies to give:

$$\boldsymbol{v_f f < \frac{2(1-\alpha)}{t_a} - v_h H} \qquad (\boldsymbol{A7})$$

10. Resist against ST (population surrenders)

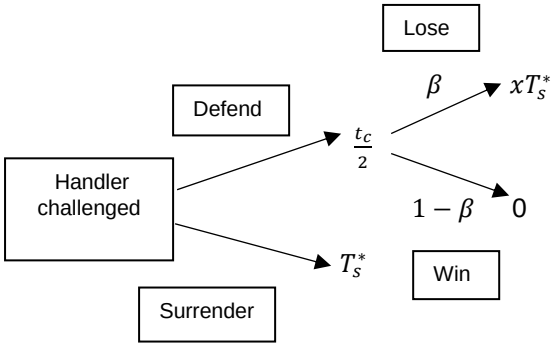


Figure 7.11. Phase diagram showing the decision points for handler that is challenged ST in a population that surrenders food items.

Following the same argument developed for situation 9 and condition A7, the conditions for Resist to be advantageous when attacked ST in a population that always surrenders food items are given by inequality 40, where the simplified search pathway from equation 37 can be substituted to give 41.

$$\frac{t_c}{2} + \beta x T_s^+ < T_s^+ \qquad (40)$$

$$\frac{t_c}{2} + \beta x \left(\frac{1}{v_f f + v_h H}\right) < \frac{1}{v_f f + v_h H} \qquad (41)$$

Which simplifies to give:

$$\boldsymbol{v_f f < \frac{2(1-\beta x)}{t_c} - v_h H} \qquad (\boldsymbol{A8})$$

Situations 11 & 12. When to resist/defend when challenged by a mutant attacker in a population that does not use kleptoparasitism

In the situation where the population does not attempt kleptoparasitism but a handler is attacked by a mutant forager, the time to acquire a food item from the start of searching, previously given as T_s and T_s^*, again simplify to the same equation, which on this occasion is just the rate at which foragers find food. In these circumstances that equation is denoted by T_s':

$$T_s' = \frac{1}{v_f f} \qquad (42)$$

11. Defend against AGG (population not using kleptoparasitism and a mutant searcher attacks the handler)

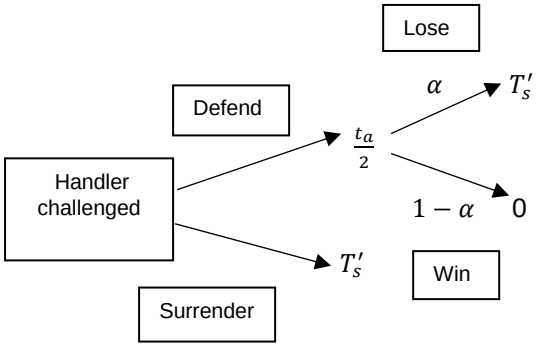


Figure 7.12. Phase diagram showing the decision points for a handler that is attacked AGG by a mutant searcher in a population which does not use kleptoparasitism.

The conditions for Defend to be advantageous in a population which does not attempt kleptoparasitism but the handler is attacked by a mutant using AGG are given by 43 and 44, incorporating the rate at which food is discovered (T_s') shown in equation 42.

$$\frac{t_a}{2} + \alpha T_s' < T_s' \qquad (43)$$

$$\frac{t_a}{2} + \alpha\left(\frac{1}{v_f f}\right) < \frac{1}{v_f f} \qquad (44)$$

Which can be simplified to give:

$$\boldsymbol{v_f f < \frac{2(1-\alpha)}{t_a}} \qquad (\boldsymbol{A9})$$

12. Resist against ST (population not using kleptoparasitism and mutant searcher attacks the handler)

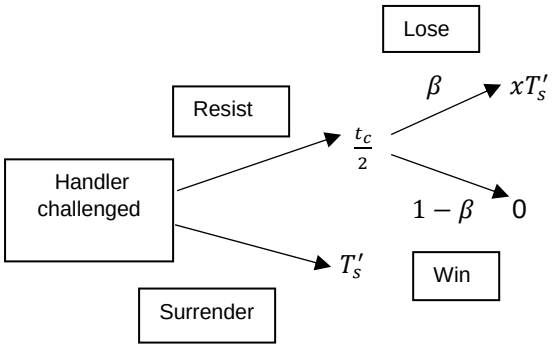


Figure 7.13. Phase diagram showing the decision points for a handler that is attacked ST by a mutant searcher in a population which does not use kleptoparasitism.

The conditions for Resist to be advantageous in a population which does not attempt kleptoparasitism but the handler is attacked by a mutant using ST are given by the inequalities shown in 45 and 46.

$$\frac{t_c}{2} + \beta x T_s' < T_s' \qquad (45)$$

$$\frac{t_c}{2} + \beta x \left(\frac{1}{v_f f}\right) < \frac{1}{v_f f} \qquad (46)$$

Which can be simplified to give:

$$\boldsymbol{v_f f < \frac{2(1-\beta x)}{t_c}} \qquad (\boldsymbol{A10})$$

In the above paragraphs I have identified the conditions when the use of kleptoparasitism by a searcher and defending/ resisting against kleptoparasitism by a handler are optimal strategies. Twelve situations, relevant to the foraging population being modelled, were considered in this second stage of the model. The associated conditions (A1a-A10) when it is advantageous to attack (AGG or ST) and to defend/ resist against attacks are summarised in Table 7.2. Appendix K gives the algebraic solutions demonstrating how conditions A1a, A1b, A3, A4, A5, A6, A7, A8, A9 and A10 were derived.

Table 7.2. Conditions under which it is advantageous to challenge and resist/ defend in the Billingsgate population.

Situation Description	Decision	Formula	Search Pathway	Solution Conditions	>
	Searcher				
Handler defends & pop'n defends	When to use AGG?	$\frac{t_a}{2} + (1-\propto)T_s < \frac{1}{v_f f}$	$T_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H}$	$\frac{2\alpha}{t_a} > \max\left(\frac{2\beta x}{t_c}, v_f f\right)$	A1a
Handler resists & pop'n resists	When to use ST?	$\frac{t_c}{2} + (1-\beta)T_s^* < \frac{1}{v_f f}$	$T_s^* = \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H}$	$\frac{2\beta x}{t_c} > \max(\frac{2\alpha}{t_a}, v_f f)$	A1b
Handler & pop'n resists/ defends	When to ignore handler	$v_f f > A1a \,\&\, A1b$	$T_s \; or \; T_s^*$	$v_f f > \max\left(\frac{2\alpha}{t_a}, \frac{2\beta x}{t_c}\right)$	A1c
Handler surrenders & pop'n surrenders	When to use AGG or ST?	Payoff is 1 whole unit of food: $\alpha = \beta = 1$	Always attack either AGG or ST	$\infty > v_f f$	A2
	Handler				
Pop'n defends & handler is an AGG forager	When to defend against AGG?	$\frac{t_a}{2} + \alpha T_s < T_s$	$T_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H}$	$v_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)v_h H$	A3
Pop'n defends & handler is an ST forager	When to defend against AGG?	$\frac{t_a}{2} + \alpha T_s^* < T_s^*$	$T_s^* = \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H}$	$v_f f < \frac{(1-\alpha)(2 + v_h t_c H)}{t_a} - \beta v_h H$	A4
Pop'n resists & handler is an ST forager	When to resist against ST?	$\frac{t_c}{2} + \beta x T_s^* < T_s^*$	$T_s^* = \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H}$	$v_f f < \frac{2(1-\beta x)}{t_c} + (1-\beta - \beta x)v_h H$	A5
Pop'n resists & handler is an AGG forager	When to resist against ST?	$\frac{t_c}{2} + \beta x T_s < T_s$	$T_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H}$	$v_f f < \frac{(1-\beta x)(2 + v_h t_a H)}{t_c} - \alpha v_h H$	A6
Pop'n surrenders	When to defend against AGG?	$\frac{t_a}{2} + \alpha T_s^+ < T_s^+$	$T_s^+ = \frac{1}{v_f f + v_h H}$	$v_f f < \frac{2(1-\alpha)}{t_a} - v_h H$	A7
Pop'n surrenders	When to resist against ST?	$\frac{t_c}{2} + \beta T_s^+ < T_s^+$	$T_s^+ = \frac{1}{v_f f + v_h H}$	$v_f f < \frac{2(1-\beta x)}{t_c} - v_h H$	A8
Pop'n doesn't attack & mutant AGG attacker	When to defend against AGG?	$\frac{t_a}{2} + \alpha T_s' < T_s'$	$T_s' = \frac{1}{v_f f}$	$v_f f < \frac{2(1-\alpha)}{t_a}$	A9
Pop'n doesn't attack & mutant ST attacker	When to resist against ST?	$\frac{t_c}{2} + \beta x T_s' < T_s'$	$T_s' = \frac{1}{v_f f}$	$v_f f < \frac{2(1-\beta x)}{t_c}$	A10

7.4.4: Stage 3: Candidate evolutionarily stable strategies (ESS's):

To fully specify the behaviour of foragers in the population we must consider what decisions they make at the four decision points described by the four strategies shown in Table 7.1, that is, the probability with which they attack AGG (p_1), the probability with which they attack ST (p_2), the probability with which a forager defends against AGG (p_3) and the probability with which they defend against ST (p_4). Following Hadjichrysanthou and Broom (2012), if the population is at or near to an equilibrium and all members follow strategy profile (p_1, p_2, p_3, p_4) that population can be invaded by foragers that use a different foraging strategy which results in a higher food consumption rate, as this would translate into a higher fitness payoff for those foragers. To consider whether a mutant playing a slightly different strategy to the rest of the population can invade the population playing strategy profile (p_1, p_2, p_3, p_4) it is sufficient to consider whether the mutant uses a different strategy at any one of the four decision points. A different strategy at any one decision point that gives a higher payoff will result in an overall higher payoff for the mutant and it is sufficient to consider differences in pure strategies at each of the four decision points. Hadjichrysanthou and Broom (2012) provided proofs for some generic parameters and conducted extensive numerical investigation of why there are no mixed-strategy ESS's. Following those arguments, consideration of the use of only pure strategies in this model means that the searcher will either always use AGG, always use ST, or always ignore the opportunity to attack. The working assumption in the current model therefore is that there are twelve candidates for pure strategy ESS's that need to be considered as outlined below. Where the four decision points are the strategies (p_1, p_2, p_3, p_4) and the probability 1 or 0 means the strategy is always used (1) or never used (0), respectively.

- Strategy (1,0,1,0) (AGG Defender): The forager always attacks AGG and always defends against AGG, but never uses or resists against ST.
- Strategy (0,1,0,1) (ST Resistor): The forager always attacks ST and always resists ST attacks, but never uses or defends against AGG.
- Strategy (1,0,0,1) (AGG Resistor): The forager always attacks AGG but only ever resists against ST attacks.
- Strategy (1,0,0,0) (AGG Marauder): The forager always attacks AGG but never resists or defends against attack.
- Strategy (0,1,1,0) (ST Defender): The forager always attacks ST and only defends against AGG.
- Strategy (0,1,0,0) (ST Marauder): The forager always attacks ST but never resists or defends against attacks.
- Strategy (1,0,1,1) (AGG Hawk): The forager always attacks AGG and always defends and resists against both types of attack.
- Strategy (0,1,1,1) (ST Hawk): The forager always attacks ST and always defends and resists against both types of attack.
- Strategy (0,0,1,1) (Retaliator): The forager never attacks but it always defends and resists against both types of attack.

- Strategy (0,0,0,0) (Dove): The forager always searches for its own food, it never attacks and never defends or resists.
- Strategy (0,0,0,1) (ST Retaliator): The forager never attacks using either strategy and never defends against AGG but always resists against ST.
- Strategy (0,0,1,0) (AGG Retaliator): The forager never attacks using either strategy, it always defends against AGG but never against ST attacks.

The twelve possible strategies listed above will be evolutionarily stable (ESS's) when different combinations of the conditions (A1a to A10) outlined in Table 7.2 are met. The combinations of conditions that result in a strategy being an ESS are shown in Table 7.3. Where an asterisk is shown there are no conditions in which the strategy is evolutionarily stable and a population using that strategy can always be invaded by a mutant playing a different strategy.

Table 7.3. Conditions that need to be satisfied for each of the twelve candidate foraging strategies to be an ESS. Conditions with a superscript means the complement of that particular condition needs to be satisfied as part of the ESS combination. An asterisk indicates there are no conditions in which the strategy is an ESS.

Strategy	Strategy Name	Conditions satisfied when ESS
(1,0,1,0)	AGG Defender	$*$
(0,1,0,1)	ST Resistor	$*$
(1,0,0,1)	AGG Resistor	$A2 \cap A8 \cap A7^c$
(1,0,0,0)	AGG Marauder	$A2 \cap A8^c \cap A7^c$
(0,1,1,0)	ST Defender	$A2 \cap A7 \cap A8^c$
(0,1,0,0)	ST Marauder	$A2 \cap A7^c \cap A8^c$
(1,0,1,1)	AGG Hawk	$A1a \cap A3 \cap A6$
(0,1,1,1)	ST Hawk	$A1b \cap A4 \cap A5$
(0,0,1,1)	Retaliator	$A1c \cap A9 \cap A10$
(0,0,0,0)	Dove	$*$
(0,0,0,1)	ST Retaliator	$*$
(0,0,1,0)	AGG Retaliator	$*$

7.4.5: Stage 4: Ecological conditions for the ESS's:

An investigation of the regions of parameter space where each of the candidate ESS's shown in Table 7.3 occur was conducted. Each ESS occurs when a system of inequalities made up by various combinations of conditions A1a to A10 are satisfied, as shown in column 3 of Table 7.3. Varying the values of the different ecological parameters contained in the inequalities had a direct influence on when those inequalities were satisfied. Although all of conditions A1a to A10 were strict inequalities, the boundary conditions where they are satisfied were obtained by setting the left and right-hand sides of the inequalities equal to each other.

The actual values of the parameters used in the model were obtained from the real foraging data from Billingsgate. These values are summarised in Table 7.4. The values used for t_h, t_c, and t_a were the results of a numerical investigation of the equilibrium densities at Billingsgate of the different behavioural compartments specified in the model. A more lengthy description of how these values were obtained and their significance is outlined in the results section on testing for equilibrium densities (Section 7.5.2). The two parameters that were allowed to vary when investigating the ecological conditions in which the ESS's occur were the rate at which foragers find food $(v_f f)$ and the total number of individuals in foraging patches (P); these were plotted graphically, on x and y axes respectively, to create a visual parameter space of ESS's for different values of the two conditions.

Table 7.4. Parameter values used to investigate the regions of parameter space occupied by different ESS's at Billingsgate.

Parameter/ Strategy	Method of Calculation	Value
$\boldsymbol{\alpha}$	Probability of winning AGG fight	0.79
$\boldsymbol{\beta}$	Probability of winning ST fight	0.71
$\boldsymbol{v_f f}$	Mean items per patch/ foragers per patch	Varied
$\boldsymbol{v_h}$	Rate at which foragers discovered/ rate at which food items discovered	0.83
$\boldsymbol{t_h}$	Investigated numerically	0.42
$\boldsymbol{t_c}$	Investigated numerically	0.14
$\boldsymbol{t_a}$	Investigated numerically	0.26
$\boldsymbol{P}$	Population Density	Varied

None of the inequalities (A1a – A10) explicitly contain the parameter P. Values for P were obtained by substituting equation 26 for H in conditions A3 to A8. These were then solved for P using Wolfram Alpha mathematical software (Wolfram Alpha©, 2016). Conditions A1a, A1b, A1c, A2, A9 and A10 do not contain the variable H. These inequalities were solved using the known values from the data recorded at Billingsgate for the various parameters making up the inequalities, this gave a value of $v_f f$ for all P values.

Inputting the real data from Billingsgate into the inequality conditions revealed that 5 of the remaining 7 candidate ESS's shown in Table 7.3 were actually possible in the parameter space of the Billingsgate environment. These 5 strategies were AGG Resistor, AGG Marauder, ST Marauder, AGG Hawk and ST Hawk. It was found that there were no regions of the foraging parameter space at Billingsgate where all the inequality conditions for the other two ESS candidates, ST Defender and Retaliator, were met, indicating that, although they were possible as ESS's, for the values of ecological parameters occurring at Billingsgate they were not ESS strategies. For the Retaliator strategy this may be explained by the fact that the probability of success for both AGG and ST, α and β respectively, were very high ($\alpha = 0.79, \beta = 0.71$) making some sort of attacking strategy worthwhile.

The inequality conditions that were set as equations and solved for P, as described above, were plotted as boundary conditions in foraging parameter space using MATLAB (Mathworks©, version R2015b). The regions of parameter space occupied by the five ESS strategies for Billingsgate are shown in Figure 7.14.

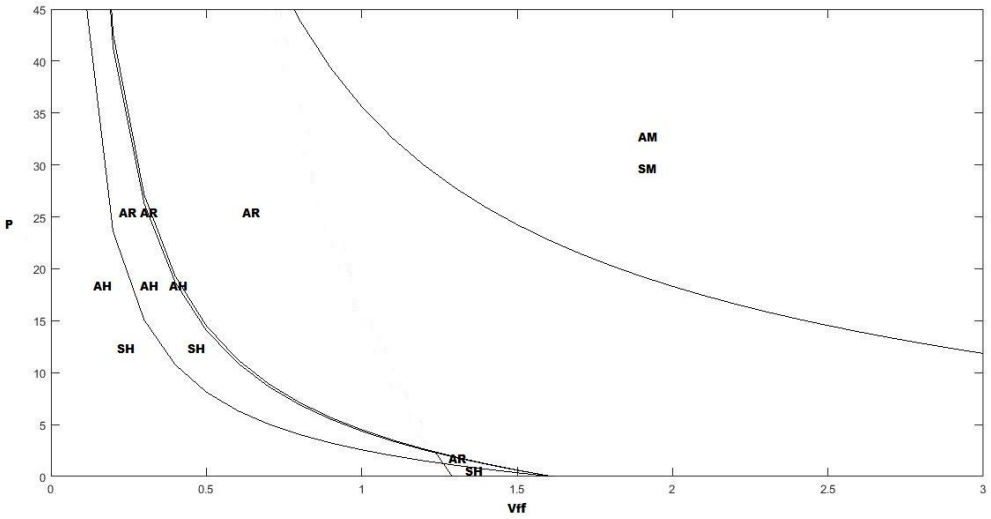


Figure 7.14. Graph showing regions of the foraging parameter space at Billingsgate where each of the 5 possible ESS's occurs for different population density values (P) and food discovery rates ($v_f f$). The five possible ESS's represented are AGG Hawk (AH), ST Hawk (SH), AGG Resistor (AR), AGG Marauder (AM) and ST Marauder (SM). Note that it is possible for more than one strategy to be an ESS in the same region of parameter space and ESS regions for different strategies overlap in some cases.

7.5 – Results

7.5.1: Analyses and treatment of Billingsgate foraging data (Obtaining values for the model):

In this results section I describe how various aspects of the model were tested using data from the foraging behaviour observed at Billingsgate. Descriptive statistics and mean values for the foraging behaviour at Billingsgate were obtained for the variables and parameters used in the model. This included mean scores for the population densities, parameters values and probabilities with which strategies were used listed in Table 7.1. These scores were obtained from data recorded for the entire year of study.

Averaging the data from Billingsgate over the year of study provided values for a number of the model parameters and strategies. The probability of an attacker winning a fight was given by the mean success rate of each kleptoparasitic strategy in the population. This was 79% for AGG giving a probability of success (α) of 0.79, and 71% for ST giving a success probability (β) of 0.71. The rate at which food was discovered at Billingsgate was calculated as the total number of items discovered divided by the total number of foragers. This gave a mean rate at which food items were discovered $(v_f f)$ as 0.71 items per searcher. The rate at which searchers encounter handlers (v_h) was calculated as the rate at which foragers were discovered to challenge as a proportion of the rate at which food items were discovered, this returned a value of 0.83, meaning that the majority of handlers were discovered by other foragers whilst they were handling a food item.

To calculate the probability of a searcher using a kleptoparasitic strategy, either attacking AGG or ST, (p_1) and (p_2) respectively upon discovering a handler, it was necessary to find some way of accounting for the proportion of occasions that foragers ignored a handler and continued searching for food items. As there is no direct way of knowing whether a searcher had the opportunity to attack and did not it was necessary to estimate ignored opportunities. This was done using the percentage of foraging patches where no kleptoparasitism occurred as a measure of ignored opportunities. Kleptoparasitism was possible in all foraging patches and the percentage of patches where no kleptoparasitism took place, 39% of patches, was viewed as a crude index of the rate at which foragers ignored opportunities to steal. The probability that a searcher attacked using either AGG or ST was then calculated by multiplying the percentage with which the particular kleptoparasitic strategy was used by the percentage of patches within which kleptoparasitism occurred (61%). This gave a probability of attacking AGG (p_1) of 0.38 and the probability of attacking ST (p_2) of 0.23. The probability that a handler defended (p_3) or resisted (p_4) was simply the proportion of attacks recorded at Billingsgate where the handler defended or resisted. Handlers at Billingsgate defended against AGG 35% of the time making p_3 0.35 and resisted against ST 64% of the time making p_4 0.64.

Values were unknown for three parameters that were approximated using exponential probability distributions: mean handling time (t_h), mean ST fight duration (t_c), and mean AGG fight duration (t_a). Plausible values for these parameters were investigated numerically using the solutions for the density of each behavioural compartment in the population at equilibrium (equations 18, 19, 20, 21, 22 and 26) and the known parameter values and behavioural compartment densities from the

foraging data for Billingsgate. Table 7.5 summarises the parameter values and probabilities for strategy use in the Billingsgate population that were inputted into the model to investigate equilibrium densities of behaviours.

Table 7.5. Mean values for model parameters obtained from Billingsgate foraging data.

Parameter/ Strategy	Method of Calculation	Value
$\boldsymbol{\alpha}$	Probability of winning AGG fight	0.79
$\boldsymbol{\beta}$	Probability of winning ST fight	0.71
$\boldsymbol{p_1}$	% use of AGG x % of patches with kleptoparasitism	0.38
$\boldsymbol{p_2}$	% use of ST x % of patches with kleptoparasitism	0.23
$\boldsymbol{p_3}$	Probability of defending	0.35
$\boldsymbol{p_4}$	Probability of resisting	0.64
$\boldsymbol{v_f f}$	Mean items per patch/ foragers per patch	0.71
$\boldsymbol{v_h}$	Rate at which foragers discovered/ rate at which food items discovered	0.83
$\boldsymbol{t_h}$	Investigated numerically	Varied
$\boldsymbol{t_c}$	Investigated numerically	Varied
$\boldsymbol{t_a}$	Investigated numerically	Varied
$\boldsymbol{x}$	Avg. portion of food item obtained by ST	0.63

The densities of behaviours in the population was also obtained from the real foraging data for Billingsgate. The mean patch size at Billingsgate was 12 birds per patch. The data showed that on average the densities of individuals in each behavioural category were: 71% searchers (S) (this equates to ~8.52 birds/patch), 21% handlers (H) (~2.52 birds/patch) and 8% were engaged in kleptoparasitic fights over food (~0.96 birds/patch). As previously stated 63% of the observed fights at Billingsgate involved AGG and 37% were ST fights. This gives values of approximately 0.6 birds per patch engaged in AGG fights and 0.36 birds per patch engaged in ST fights. As fights involved exactly one kleptoparasite and host, the ~0.6 birds engaged in AGG fights is split 50:50 between aggressive attackers (A) (~0.3 birds/patch) and defenders (D) (~0.3 birds/patch) and the remaining ~0.36 birds engaged in ST is split 50:50 between stealth attackers (C) (~0.18 birds/patch) and resistors (R) (~0.18 birds/patch). The density of individuals in each behavioural compartment at Billingsgate as an average proportion of a patch of 12 foragers is listed in column 4 of Table 7.6.

7.5.2: Testing for equilibrium densities:

The parameter values listed in Table 7.5 were used to investigate whether the density of individuals that occurred in behavioural compartments at Billingsgate could be at an equilibrium. Numerical investigation showed that in order for the densities of individuals observed in the foraging population at Billingsgate (shown in Table 7.6 column 4) to be at an equilibrium, using the known parameter values and strategy probabilities for that population, then the mean handling time for food

items (t_h), mean duration of ST fights (t_c) and mean duration of AGG fights (t_a) must be: $t_h = 0.42, t_c = 0.14, t_a = 0.26$. Appendix I (Section I.2) outlines detailed algebraic solutions that gave the parameter values for t_h, t_c and t_a.

Assuming a foraging population of 12 individuals at patches, the above values for t_h, t_c, and t_a along with the parameter values shown in Table 7.5, were inputted into equations 18, 19, 20, 21, 22 and 26. The quadratic formula (26) giving the equilibrium number of handlers was solved first, followed by 18 giving the equilibrium number of searchers and then 19, 20, 21 and 22 giving the equilibrium number of ST attackers, resistors, AGG attackers and defenders respectively. The solutions resulted in equilibrium densities close to the densities of individuals in each compartment observed in the Billingsgate population, as shown in Table 7.6 column 3.

Table 7.6. Equilibrium density results for the Billingsgate population at parameter values of $(\boldsymbol{t_h = 0.42, t_c = 0.14, t_a = 0.26})$. Column 3 shows the density of each compartment at equilibrium for these parameter values, column 4 shows the density of each compartment actually observed at Billingsgate.

Behavioural Compartment	Equilibrium Solution	Equilibrium Density	Billingsgate Densities
Handlers $(\boldsymbol{H})$	$H = -(p_1p_3t_a + p_2p_4t_c)v_hH^2 - (1 + t_hv_ff)H + t_hv_ffP$ $H = -0.04303944H^2 - 1.2982H + 3.5784$	≈2.53	2.52
Searchers $(\boldsymbol{S})$	$S = \frac{H}{t_hv_ff}$ $S = \frac{2.54217}{0.2982}$	≈8.5	8.52
ST attackers $(\boldsymbol{C})$	$C = \frac{1}{2}\frac{p_2p_4t_cv_hH^2}{t_hv_ff}$ $C = \frac{0.09627144737}{0.5964}$	≈0.18	0.18
Resistors $(\boldsymbol{R})$	$R = \frac{1}{2}\frac{p_2p_4t_cv_hH^2}{t_hv_ff}$ $R = \frac{0.09627144737}{0.5964}$	≈0.18	0.18
AGG attackers $(\boldsymbol{A})$	$A = \frac{1}{2}\frac{p_1p_3t_av_hH^2}{t_hv_ff}$ $A = \frac{0.181876456}{0.5964}$	≈0.31	0.30
Defenders $(\boldsymbol{D})$	$D = \frac{1}{2}\frac{p_1p_3t_av_hH^2}{t_hv_ff}$ $D = \frac{0.181876456}{0.5964}$	≈0.31	0.30

The results in Table 7.6 for parameter values $t_h = 0.42, t_c = 0.14, t_a = 0.26$ not only gave equilibrium densities close to the densities observed in the Billingsgate foraging population but returned ratios of AGG to ST in line with the rates with which these strategies were used by foragers at Billingsgate. This indicated that the duration of an ST fight to an AGG fight, at the values of t_h, t_c and t_a given in Table 7.6 and identified through numerical investigation, accurately captured the ratio of these two strategies in the real foraging population, this being that the mean duration of an AGG fight was nearly twice that of an ST fight.

7.5.3: Comparing strategy use at Billingsgate with ecological conditions for ESS's:

To identify the strategies used by foragers at Billingsgate focal animal observations were conducted using video recordings of foraging patches. Individual foragers were observed as they moved around the patch and a continuous record was made of their foraging behaviours, indicating whether they sampled for food items, attacked using AGG, attacked using ST and, when handling, whether they defended, resisted or surrendered against attacks by other foragers. These focal animal observations were used to build up a picture of the forager's behaviour and to attribute a strategy to the forager based on the ESS strategies outlined in Table 7.3.

A total of 189 focal animal observations were completed. As these focal animal analyses consisted of observations of wild foraging birds there was considerable variation in how long a bird could be observed before it was lost from view. Descriptive statistics for the duration of focal observations are shown in Table 7.7. The duration for which an individual was observed was recorded in seconds and varied from 3 seconds to 650 seconds (Range: 647). A Shapiro Wilk test of normality on the data for duration of focal animal observations showed that it was significantly non-normally distributed ($W=0.76$, $p<0.001$), so the median of 60 seconds was the measure of central tendency that probably best reflected the duration of the focal animal observations conducted.

Table 7.7. Descriptive statistics showing duration of focal animal observations on foragers at Billingsgate.

Duration (Seconds)	Statistic
Samples	189
Minimum Duration	3
Maximum Duration	650
Range	647
Mean	102.48
Standard Deviation	108.35
Median	60

Successfully attributing a strategy to an individual forager required the observation of interactions by that forager as both a searcher and handler. For a strategy where the forager never engages in a type of behaviour, such as Retaliator where the searcher never attacks, a minimum observation period of 300 seconds was used. This was viewed as a sufficiently long period of time to allow the focal animal's behaviour to be observed in multiple interactions. None of the individuals observed met this threshold for duration so strategies such as Dove or Retaliator were not attributed to any birds. As neither of these strategies are ESS's in the ecological conditions at Billingsgate this was essentially a moot point but is reported here as it formed part of the method used for attributing strategies. From the 189 observations conducted it was possible to confidently attribute a strategy to 52 foragers. The strategies used by these 52 foragers were considered against the ecological conditions (rate of food discovery ($v_f f$) and population density (P)) in the patches in which they were

observed. This permitted the strategies to be plotted against ecological conditions in the parameter space described for Billingsgate in Figure 7.14.

Of the 52 foragers attributed strategies it was found that 12 of those foragers were using strategies in the correct region of parameter space to make them ESS strategies and 40 foragers were using their strategies in the wrong region of parameter space. This means that ~23% of foragers at Billingsgate were making optimal foraging decisions and individually using an ESS strategy. As there were five possible ESS strategies and these strategies occupied five regions of parameter space, in the ecological conditions found at Billingsgate, this percentage of foragers using an ESS (23%) was slightly higher than would be expected by chance (20%). Figure 7.15 shows the 12 correctly used ESS foraging strategies plotted in parameter space and Figure 7.16 shows the location of the 40 foraging strategies used in the wrong regions of parameter space.

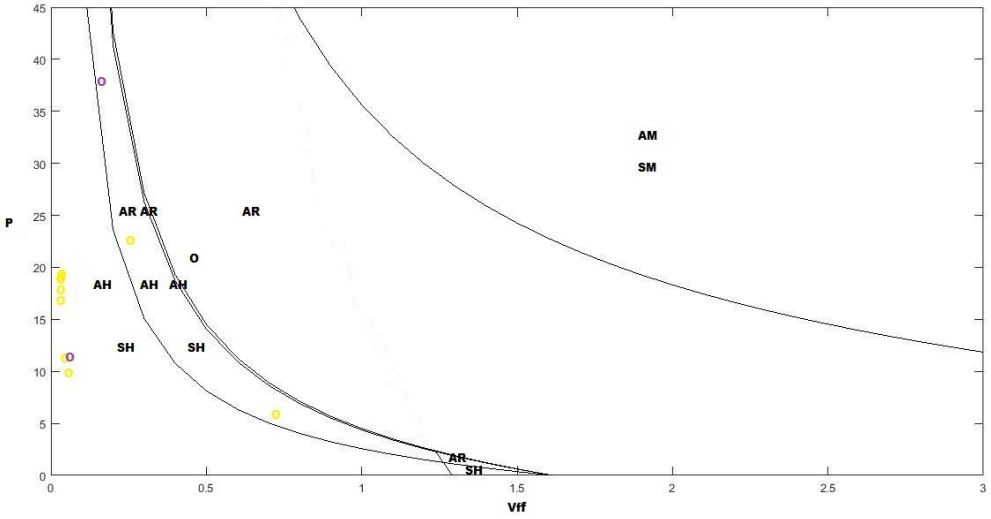


Figure 7.15. Foraging strategies used in the region of parameter space in which they are ESS's. Each circle represents one of the 12 foragers making the optimal foraging decision. Strategies are colour coded: AR (black), AH (yellow), SH (purple).

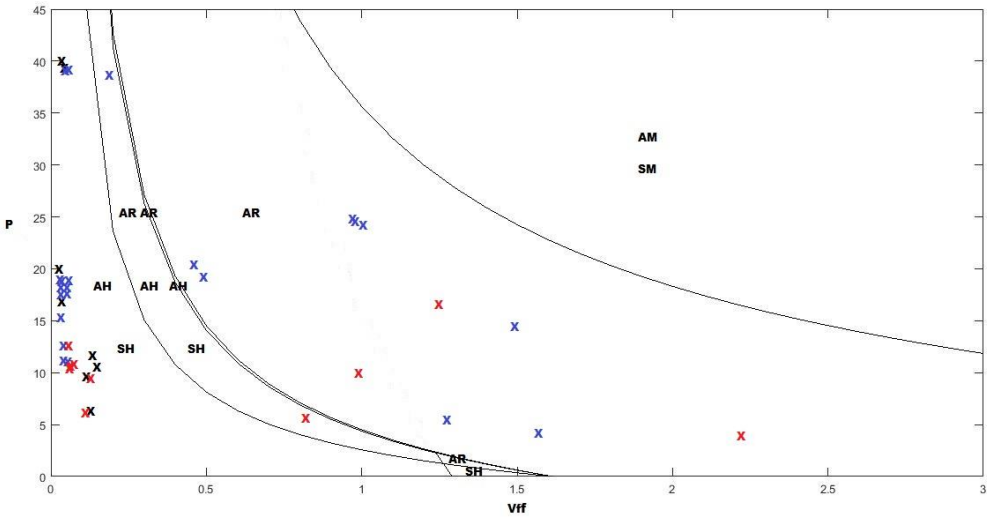


Figure 7.16. Foraging strategies used in the region of parameter space in which they are not an ESS. Each X represents a forager that is using a strategy other than the ESS strategy for that region of parameter space (N=40). X's are colour coded by the strategy used: AR (black), AM (blue), SM (red).

Considerable variation was seen between strategies in the rates with which they were used and the rates with which those strategies were correctly and incorrectly used. Of the 52 foragers to whom strategies could be attributed, ST Hawk (SH) was the least used strategy being used on only 2 occasions, on both occasions this strategy was used in the correct region of parameter space where it was an ESS. The most used strategy was AGG Marauder (AM). This strategy was used on 22 occasions, on all occasions where it was used it occurred in regions of parameter space where it was not an ESS. On 14 of those occasions it was used in the region of parameter space where AGG Hawk and ST Hawk were ESS's, indicating that foragers using AGG Marauder were correctly attacking handlers using AGG, but failing to defend their food items when attacked in a region of parameter space where food was scarce and defensive strategies were optimal.

AGG Resistor (AR), ST Marauder (SM) and AGG Hawk (AH) were each observed 9, 10 and 9 times respectively. In the vast majority of these cases AGG Resistor and ST Marauder (SM) were strategies used in the region of parameter space where they were not an ESS, with AGG Resistor being used in the wrong region on 8 occasions (~88%) and ST Marauder also used in the wrong region on all 10 occasions (100%). All observations of AGG Resistor in the wrong region of parameter space occurred in the region where AGG Hawk and ST Hawk were the ESS's. Foragers using this strategy made the error of failing to defend against AGG attacks by other foragers, despite attacking AGG and resisting against ST.

The erroneous use of ST Marauder occurred mostly in the region of parameter space where AGG Hawk and ST Hawk were ESS's. Like those using AGG Marauder these foragers failed to resist and defend food items in a region of parameter space where food was scarce and defensive behaviours to try and keep what food you have were optimal. In contrast AGG Hawk was used in the

correct region of parameter space on all 9 occasions (100%) that it was used, making Hawk strategies (both ST and AGG Hawk) the most effectively used strategies by individuals making optimal foraging decisions and using an ESS. Table 7.8 shows the frequencies with which strategies were used in regions of parameter space where they were and were not ESS's.

Table 7.8. Frequency with which strategies at Billingsgate were used in the region of parameter space where they were an ESS and regions where they were not an ESS.

Strategy	ESS region	Non-ESS region
AGG Resistor	1	8
AGG Marauder	0	22
ST Marauder	0	10
AGG Hawk	9	0
ST Hawk	2	0

7.6 – Discussion

This model was developed to try and capture the kleptoparasitic behaviours of a population of foraging gulls at Billingsgate Market and then to investigate what the model, when tested against the real foraging behaviour recorded at Billingsgate, could tell us about the optimality and stability of the behavioural decisions made by individuals in that population. This was pursued in two ways: 1. By considering the density of individuals engaged in each behaviour of interest in the population and investigating the possibility that these behaviours were at equilibrium densities. 2. Through assessing the optimality of the behavioural decisions of individual foragers when compared against the ecological conditions in the patches in which they were foraging. Were foragers using ESS strategies?

7.6.2: Equilibrium densities: The values of a number of the model parameters were known from the real foraging behaviour at Billingsgate. The values for handling time (t_h), ST fight duration (t_c) and AGG fight duration (t_a) were unknown and were varied to investigate numerically at what values of these parameters the model produced equilibrium densities that matched the densities of behaviours observed at Billingsgate. The values arrived at were: t_h=0.42, t_c=0.14, t_a=0.26. The important question to ask about these values is whether they are plausible values for the parameters they represent.

Considering first the fight duration variables t_c and t_a. At the reported values the duration of an AGG fight (t_a) was twice that of an ST fight (t_c). This fits with our understanding of these two kleptoparasitic strategies. Stealth kleptoparasitism by name and definition is a sneaky strategy that involves less of an interaction between attacker and handler and in many cases that interaction was over before the handler could respond effectively and escalate to a protracted fight. In contrast AGG as a strategy actually required the attacker to engage in a fight with the handler to try and take the food item by strength. In light of this, the finding that the duration of an AGG fight was twice that of an ST fight was reasonable and the fact that the values that produced the equilibrium densities (t_c=0.14, t_a=0.26) delivered the correct ratio of AGG (~65%) to ST (~35%) as observed in the Billingsgate population was reassuring.

When considering whether these values accurately represent the mean duration of fights in the Billingsgate population it was noted that fights at Billingsgate, even AGG fights, were short in duration. Over the year of study no significant injuries were sustained by birds engaged in fights over food. Gulls often sustain injuries whilst fighting and fights can last for a considerable length of time particularly during the breeding season when they are generally more aggressive. The fact that no observations of injuries were made over the period of study at Billingsgate may reflect that, on the whole, there is no shortage of food at the site so the conditions that would make staying in a lengthy fight a good economic decision might not have existed.

If the values of t_c and t_a are viewed as time measured in seconds then they may be too short to be plausible values for fight duration at Billingsgate. However, if they are viewed as a measurement of time in minutes, which was how patch duration at Billingsgate was recorded, this would make t_c

(0.14 x 60) 8.4 seconds and t_a (0.26 x 60) 15.6 seconds. These would be more realistic mean fight times and more representative of the real behaviour seen at Billingsgate.

The value arrived at for mean handling time, t_h=0.42, could also be measured in seconds or minutes. The first of which would make the mean handling time less than half a second, meaning searchers would have had to act exceptionally fast to identify and challenge handlers before they finished handling and consumed food items. This seems unrealistic and does not fit with what is known about food in the Billingsgate environment, which contained an abundance of larger food items all of which could reasonably be expected to take longer than 0.5 seconds to handle. Considering the value of t_h as a proportion of a minute (0.42 x 60) gives a mean handling time of 25.2 seconds. As with the fight duration times, measuring t_h in minutes provides much more plausible values and may more accurately reflect the mean times for which birds handled food before being challenged or fully consuming food items.

Using the values for t_h, t_c and t_a to accurately draw conclusions about whether the densities of behavioural compartments at Billingsgate were at an equilibrium depends on whether the system of dynamical equations, set out in stage 1 of the model (equations 2, 3, 4, 5, 6 and 7), included and captured all variables that influenced behaviour in that environment. As stated in the introductory comments to this chapter, the lack of competitor species and other trophic levels at Billingsgate made it a good natural laboratory in which to try and meet the simplifying assumptions needed for a mathematical model. Whether the densities of behavioural compartments at Billingsgate are at an equilibrium and if the model described here captures and demonstrates this depends on how the values of the time parameters t_h, t_c and t_a are interpreted as described in this discussion section. None of the values arrived at by numerical investigation were at wildly unrealistic levels and the differences between t_c and t_a accurately captured the ratio of AGG to ST use at Billingsgate, meaning the model may provide a good approximation of the densities of behaviours seen in the real foraging population.

The fact that there has been a foraging population at this site since the early 1980's and over that time the population, and the availability and scheduling of food, is likely to have remained relatively stable makes it a realistic possibility that the population may have settled at some equilibrium of searchers to handlers to kleptoparasites. Hopefully the model developed and tested here has improved our understanding of and accurately described the density of behaviours in the Billingsgate foraging population.

7.6.3: Use of ESS strategies: The focal animal analyses conducted to assess individual use of ESS's showed that only 23% of the 52 foragers to whom strategies could be attributed were actually playing an ESS. This is slightly above the level expected to be using an ESS by chance and seems to indicate that gulls at Billingsgate were on the whole not making good behavioural decisions. There are, however, a number of possible explanations for this poor result.

First, the method used for attributing strategies was limited in a number of ways. The focal animal observations involved wild foraging birds. This meant that I had no control over the duration for which birds could be observed and the interactions that occurred in the foraging patch could not be manipulated experimentally. Birds could come and go as they pleased so many of the focal animal observations were of too short a duration to confidently attribute a strategy to the forager. It was also not possible to ensure that all the necessary interactions as both searcher and handler actually occurred to allow confirmation that a particular strategy was being used by a forager. A large number of focal animal observations had to be discounted and some strategies could have been incorrectly attributed to foragers based on insufficient observation time.

Second, perhaps more significantly, the one-species approach used to model this population assumed that all foragers were essentially identical and that averaging the data for the whole year of study would successfully smooth out the influence of competitive asymmetries between individuals and between the 3 study species. However, beyond the ecological parameters of food discovery rate ($v_f f$) and density of the population in a patch (P) that were the focus of this analysis, asymmetries between foragers of different species clearly did affect the foraging decisions made. For example, the more aggressive Hawk strategies (AGG Hawk and ST Hawk) were the strategies used effectively and played as ESS's the majority of the time. These are likely to be strategies used by the larger, more dominant species. In contrast, the Marauder strategies (ST Marauder and AGG Marauder) were strategies used in the wrong regions of parameter space a majority of the time. These strategies were seen most frequently in the region where AGG Hawk and ST Hawk were ESS's, indicating that foragers were failing to defend food items when such behaviour would have been optimal. What appeared to be sub-optimal behaviour of surrendering food, in a region where food was scarce and defensive behaviours were predicted by the model, in most cases will have been the best behavioural decision for some handlers, given the competitive advantages of the bird that was attacking it. For example, due to differences in size and strength it was never optimal for a BHG handler to defend against a GBB. The asymmetries between these two species are based on size dimorphism and are clear for all individuals to see. As argued by Maynard Smith (1982), when individuals are aware of asymmetries those asymmetries will affect behaviour. The one-species model developed here was unable to account for the fact that the optimal behaviour in a given region of parameter space would differ between the 3 study species due to differences in competitive ability; and the modelling assumption of only considering pure strategies, as a forager can only have one strategy that is its best decision, overlooked the fact that the best decision a handler can make may change as a function of the species of opponent.

The one-species approach was used to keep the model as simple as possible and make the necessary mathematics more tractable. The regions of parameter space predicted by the model make intuitive sense and agree with previous models (Broom, Luther & Ruxton, 2004; Hadjichrysanthou & Broom, 2012), with ESS regions for Hawk strategies in low food availability patches and Marauder strategies in areas of higher food availability where defensive behaviour is less necessary as new food items are encountered frequently. Unfortunately, the model failed to accurately predict individual

foraging decisions because the regions of ESS parameter space will differ between species and may not match the regions produced by this model. Rather than foragers at Billingsgate making poor foraging decisions it is actually the case that the model was too general and failed to capture that the optimal behavioural decision will differ by species throughout parameter space and as a function of opponent. A more complex three-species model is required to accurately investigate the optimality of individual foraging decisions in the population at Billingsgate.

7.7 – Summary

In this chapter I have developed a game-theoretical model of kleptoparasitic behaviour in a population of the same size as the urban gull population at Billingsgate. The one-species model developed here for comparison against the real foraging population at Billingsgate may capture and accurately describe general population level patterns of behaviour such as the densities of the different compartments of foraging behaviour. However, the model was too general to draw any conclusions about the optimality of foraging decisions made by individuals in the population and a three-species model is needed to capture the complexity of the behaviours seen in the Billingsgate foraging environment. In the next chapter I will move on to summarise and provide a concluding discussion of the findings of the four studies conducted for this research thesis.

(8)

Chapter 8 – General summary and concluding remarks

8.1 – General summary of the research studies

The aim of this thesis was to investigate kleptoparasitic foraging behaviour in competitively asymmetric aggregations of gulls, with particular emphasis on investigating such behaviour in an urban population. Research was conducted at two study sites, Billingsgate, London, UK was the urban site and Brancaster, Norfolk, UK was the coastal site. Four studies were conducted to investigate behaviour in these populations.

Study 1 assessed differences in the rate of kleptoparasitism between Brancaster and Billingsgate and the ecological predictors of that difference. Kleptoparasitism was significantly greater at Billingsgate and a higher population density and the greater abundance of large food items were the best predictors of this difference. These results were considered against the background of gull population trends in the UK, where gull species are declining overall but increasing in urban areas. Kleptoparasitism was suggested as a behaviour that may help gulls meet their energy needs when environmental conditions change and as such may help gulls to inhabit a diverse range of environments and aid the invasion of urban spaces by these birds.

More work is clearly needed to develop our understanding of urban gull populations, particularly following increasing UK media reporting of agonistic interactions between humans and urban gulls (Why are there so many seagulls in cities? 2012). The urban population at Billingsgate was stable but none of the individuals in this study were marked or tracked, so it is not possible to know how truly urban the Billingsgate population is. Gulls can range over large areas in a single day and work to investigate whether the urban gulls at Billingsgate forage in a variety of habitats or have become specialised, and obtain all their food sources in urban environments by exploiting anthropogenic waste, would be helpful. Anecdotally I noted that there were large numbers of chicken bones on the rooves of buildings at Billingsgate, suggesting a large dependence on anthropogenic waste by these birds but not necessarily all acquired at this one site, as chicken is not a product sold in the seafood market at Billingsgate.

Study 2 was an investigation of the main patterns of behaviour within the study populations. I assessed which species and age-classes kleptoparasitised each other and which kleptoparasitic strategies were used. The results showed that larger species used aggressive kleptoparasitism against smaller species and smaller species used stealth kleptoparasitism against larger species. It was also found that against conspecifics gulls at Billingsgate mixed their strategy use at

approximately 3 aggressive kleptoparasitic attempts to 1 stealth kleptoparasitic attempt. This ratio was consistent across species and suggested that conspecific kleptoparasitism in this population may have settled at a mixed strategy Nash Equilibrium (Nash, 1951). However, without knowing the payoffs and costs influencing the bird's decisions it was not possible to mathematically confirm whether this ratio of aggressive kleptoparasitism to stealth kleptoparasitism was actually a Nash equilibrium.

As described above, an investigation of strategy use by different species suggested that smaller species will use stealth against larger, more dominant species and will also immediately surrender food items when challenged by larger and more dominant species. This was suggested as an empirical demonstration of a Marauder strategy (Broom, Luther, Ruxton & Rychtar, 2008) or strategy X (Maynard Smith, 1982), which Maynard Smith (1982) described as paradoxical and for which he could cite no example in nature. More work would be needed to confirm empirically the existence of a Marauder strategy. That research should look further at species that can use multiple kleptoparasitic strategies to see if the use of a Marauder strategy is consistent across other areas of asymmetry, such as age-class and sex differences within species such as raptors.

Study 3 investigated what other behaviours, beyond kleptoparasitism, subordinate foraging gulls in mixed-species aggregations use to compete for resources. This question was assessed at Billingsgate due to the greater mix of age-classes in that populations as nearly all foraging gulls at Brancaster were adults. The results indicated that subordinate birds spent longer foraging, stayed closer to locations where food most consistently appeared, arrived at food patches first and took more risks to obtain food. The population was dichotomised into two categories of status: subordinate and dominant foragers, based on species differences and developmental differences in foraging ability due to age. This categorisation may have been artificial and contrived but is believed to have effectively captured differences in competitive ability in this population.

To assess latency to arrive at food and willingness to take risks gulls were provisioned with food of known size and value. More could be done with this data to assess the optimality of decisions in each status category. This would provide insights into whether individual foragers were choosing food items based on their size or calorific value and if they were prioritising the highest value or best items given their competitive abilities and the risk of having their food item stolen. Some items had higher value but would also take longer to handle than other items, so the optimal decision each individual should make may differ depending on their species and age-class.

Study 4 involved the development of a game-theoretical model of kleptoparasitism in the Billingsgate population. In this study I created a model to describe a population of the same size and able to use the same kleptoparasitic strategies as the foragers at Billingsgate. This was then compared with the real kleptoparasitism foraging data from Billingsgate.

The model assumed a population of individuals from 1 species, this was essential to make the mathematics more tractable and to assess whether it was possible to solve the system of equations which described the model population. A compartmental modelling approach pioneered by Broom and

colleagues (Broom & Ruxton, 1998; Broom, Luther & Ruxton, 2004) was used and this study represented a unique attempt to compare this theoretical approach to modelling kleptoparasitism with real foraging data.

There were two aspects to the model. The first examined whether the density of different foraging behaviours in the population could be at an equilibrium. This was investigated numerically using known parameter values from Billingsgate to try and find plausible values for parameters for which no value was available. The second aspect of the model assessed whether individual foragers were using strategies in patches with environmental conditions that would make those strategies evolutionarily stable (ESS – See Appendix B).

The results showed that, averaging the data for the whole year, the population level patterns of behaviour, these being the equilibrium densities of behaviours in the population, produced plausible values for unknown parameters, suggesting that the Billingsgate population may be at or near an equilibrium. A foraging population of gulls has been present at this site for at least 30 years making it a realistic possibility that over time the population has settled at an equilibrium of searchers to handlers to kleptoparasites.

The results for the second aspect of the model, looking at individual foraging decisions, were much more limited. The majority of individual foragers to whom strategies could be attributed (77%) did not use an evolutionarily stable strategy (ESS). Of the 23% of foragers that did use an ESS, the majority were individuals using more aggressive 'Hawk' strategies. All hawk strategies (ST Hawk and AGG Hawk – See chapter 7, section 7.3.4) were used in the correct region of parameter space, or the correct environmental conditions that would make them evolutionarily stable. The limited success with this aspect of the model was the result of using a 1 species modelling approach to describe a population of 3 species. The model failed to account for the fact that individual strategy use would be influenced by competitive differences between species. Further work is planned to develop a 3 species model of the Billingsgate population to see if this provides a more accurate assessment of the behavioural decisions made by individual foragers in this population.

8.2 – Critical appraisal of the research

To consider first the fieldwork aspects of the research conducted for this thesis. Fieldwork was conducted over a full calendar year at both study sites. Three days per month were spent collecting data at each site so a good quantity of field data was obtained for analysis for the four main studies. This data was, however, all collected by one person and whilst the quality of the data is believed to be of a high standard, fieldwork sessions at both study sites required extensive multitasking in order to record all the various behavioural, population and ancillary measures that were of interest. This will inevitably have meant that some behaviours of interest were missed and there will have been some loss of quality in the data as it was not possible for one observer to be monitoring multiple measures at all times. This was particularly true at Brancaster, the study area for which covered a large expanse of beach. Video recording of patches for later analysis did resolve some of the issue of multiple data

collection tasks sometimes occurring simultaneously, but if further fieldwork of this nature were pursued at these study sites then additional observers and research assistants would be beneficial.

Whilst discussing field sites critically, special mention should be given to the study site at Billingsgate. This site had a number of unique features some of which were exploited effectively in this research, such as the lack of competitors and trophic levels making it a useful site to meet the simplifying assumptions needed for a mathematical model. However, the fact that the site was a seafood market sustaining an urban gull population made it distinctly different from many other gull populations in urban areas, as the gulls at Billingsgate exploit a largely high quality food resource of seafood waste and discards. With this in mind caution should be exercised when generalising the findings of this research to other urban gull populations.

Despite the above there are still many interesting questions to be answered about the Billingsgate gull population that were not touched upon by this research. The marking and tracking of individuals in the population was not undertaken, such work would provide useful insights into how truly urbanised this population is and would reveal interesting things about the behaviours of juvenile gulls for whom this is their natal colony. The large number of juvenile gulls at Billingsgate fosters the impression that it may be a nursery for poor foragers. This idea seems particularly plausible when considered against the population composition observed at Brancaster which consists largely of adult birds. Longitudinal research tracking what happens to juvenile birds from Billingsgate over a number of years would enhance our knowledge of whether gulls born in urban environments such as this become specialised urban dwellers or whether they develop into foraging in marine environments and in foreshore areas as they mature and their foraging skill increases.

It is also worth reflecting critically on the fact that, for this thesis, Billingsgate was the primary population of interest and Brancaster was considered to be a baseline population for comparison. The assumption being that Brancaster was in some way typical of the shoreline foraging environments encountered by gulls throughout much of their evolutionary history. While this is a reasonable working assumption when comparing the kleptoparasitic behaviours observed at these two sites, it is also true that as these are wild bird populations I had no control over the composition of the two populations. The differing species composition of the two study sites will no doubt have created different behavioural dynamics between individuals in the population. Little can be done about this and it may not have been possible to find a coastal foraging population of gulls that only contains the three gull species that occur at Billingsgate, as new species can arrive at and begin exploiting a food resource at any time. With this in mind it is believed that Brancaster was as good a comparison population as any but it is worth acknowledging that differences between the study populations were an inevitable limitation of fieldwork.

A further limitation of this research relates to the extent to which it is possible to generalise about differences in kleptoparasitic behaviour between environments by comparing only one urban and one coastal site. The decision to focus on only one of each site was obviously dictated by resources and time availability. Ideally a comparison of research conducted at a number of coastal

and urban sites would have provided a more credible assessment of differences in the use of kleptoparasitism across environments. However, identifying suitable urban populations is not straightforward. As mentioned above, Billingsgate itself was unique in a number of ways, but was a stable population exploiting anthropogenic resources in an urban space. Many other gull populations described loosely as urban may in fact be coastal populations that exploit human structures and occasionally steal food from humans whilst, on the whole, foraging in the normal way for a coastal gull; or they may be a seasonal phenomenon, where the population exploits the roofs in an urban area as a nesting colony during the breeding season. These differences between urban populations do not rule them out as study populations for investigating the use of kleptoparasitism in urban environments but it does highlight the difficulty that exists in clearly demarcating what constitutes an urban gull population.

The use of only one study site for each environment also raises the issue of independence of observations. The unit of interest, or the replicate, for this research was the individual kleptoparasitic event. However, the population sizes differed between Billingsgate and Brancaster. The population size for Brancaster was very large, the total number of birds recorded in headcounts over the year of study was 23,263. Many of these birds will have been migrants stopping to feed at different times of the year, meaning the possibility is very low that the 100 kleptoparasitic events that occurred involved multiple recordings from the same individuals. In contrast, the total number of birds recorded over the year of study at Billingsgate was 6384. The population at Billingsgate was much more stable with many individuals residing on buildings surrounding the site year round. The mean daily population size at Billingsgate was 40 birds, thus increasing the likelihood of pseudo-replication of kleptoparasitic events.

Inevitably, of the 595 kleptoparasitic events recorded at Billingsgate, some of these will have been kleptoparasitism committed by the same individuals. This situation makes it difficult to assess whether the kleptoparasitism seen at Billingsgate reflects the use of this strategy in the environment or a consistent behavioural specialisation by certain individuals. Assessing the extent of the pseudo-replication problem at Billingsgate is difficult without a substantial marked or ringed population to allow individuals to be accurately identified.

However, one colour-ringed Herring gull (HG: *Larus argentatus*) and two colour-ringed Black-headed gulls (BHG: *Chroicocephalus ridibundus*) were recorded at Billingsgate (See Appendix N). The HG was ringed at Pitsea landfill site in Essex, UK approximately 30 miles away from Billingsgate. I recorded the presence of this bird at Billingsgate on six occasions over the year of study. Thus, this bird was an occasional visitor seen on 6 out of 33 occasions, or 18%, of field days. The two BHG were ringed in the Netherlands, I saw one of these birds twice (2/33 ≈ 6%) and the other on only one occasion (1/33 ≈ 3%) on days when field work was conducted. Observations of these three birds may provide a measure of the extent of the pseudo-replication problem through a very crude estimate of how often the same birds are being recorded at the site. If nothing else they do provide an indication that, despite the apparent stability of the size and species composition of the population at Billingsgate, this population is not fixed and there is immigration and emigration occurring at the site.

If the rate at which the colour-ringed HG was re-sighted is taken as an estimate of the pseudo-replication level in the data collected at Billingsgate then it is possible that as many as one in five kleptoparasitic events may not be independent observations.

The analyses pursued for the four studies conducted for this thesis represent the questions that were of interest to me when I started this work, culminating in my application of a model of evolutionary game theory to a real foraging population. The analyses conducted reflect my decisions regarding what data I felt was necessary to address each question. The questions addressed were not exhaustive and many other analyses could be conducted with the dataset that was generated by this research project. In some cases other methods could have been used to conduct the same analyses and these method may have been more effective. For example, some of the parameters used in the game theory model of study 4 were unknown or were estimated using probability distributions. This was the case for the parameters of handling time for food items and the durations of stealth and aggressive fights. Accurate values for these parameters may have been obtained through the use of observer software that can give very accurate measurements of the duration of behavioural events at the level of milliseconds. However, such methods are avenues for further research and I feel the executive decisions I made about what to analyse and how were sound decisions given the questions I sought to address.

8.3 – Concluding remarks

This investigation of foraging behaviour in competitively asymmetric kleptoparasitic aggregations of gulls has shown that kleptoparasitism is an important foraging strategy for gulls in urban environments. That gulls will utilise kleptoparasitism in a flexible way depending on environmental conditions and, as they can use multiple kleptoparasitic strategies, they will adjust their strategy based on an assessment of the opponent they are trying to steal from and the likelihood of success.

It is proposed that the stealth kleptoparasitic behaviours of subordinate foragers in the study population at Billingsgate may provide an empirical example of a Maruader strategy (Broom et al. 2008) or strategy X (Maynard Smith, 1982). This was a strategy whose existence was first described theoretically in the Hawk/ Dove/ Bourgeois/ Strategy X model developed by Maynard Smith (1982) but is a behavioural strategy that had not been demonstrated in real populations in nature.

The game-theoretical model of kleptoparasitism in the Billingsgate population developed in this thesis represented a novel attempt to apply the compartmental modelling approach pioneered by Broom and colleagues to a real foraging population and real data on kleptoparasitism. This model proved successful at explaining some aspects of foraging behaviour at a population level but proved limited in assessing how good the foraging decisions were of individuals in the population. Further research could improve the explanatory power of this model through the development of a 3 species model.

It is hoped that this work has made a valuable contribution to the application of evolutionary game theory models to real foraging populations and has also provided useful insights into the foraging behaviours of gull species, particularly populations of gulls in urban environments. As the ecological conditions faced by many gull species change, as a result of human activity, and their survival becomes more precarious (Eaton et al. 2015) knowledge of their behaviour and foraging abilities will be essential to their conservation.

References

Alcock, J. (2005). *Animal Behaviour* (8th ed.). Sunderland MA. Sinauer Associates Inc.

Association for the Study of Animal Behaviour. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, 83, 301-309.

Barnard, C.J. (1984). *Producers and Scroungers: Strategies of exploitation and parasitism*. Beckenham, Kent. Croom Helm.

Barnard, C.J. & Sibly, R.M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29, 543-550.

Barnard, C.J. & Thompson, D.B.A. (1985). *Gulls and plovers: the ecology of mixed-species feeding groups*, London, Croom Helm.

Barta, Z. & Giraldeau, L-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype limited producer-scrounger game. *Behavioural Ecology and Socoibiology*, 42, 217-223.

Bertellotti M. & P. Yorio 2000. Age-related feeding behaviour and foraging efficiency in Kelp Gulls *Larus dominicanus* attending coastal trawlers in Argentina*. Ardea*, 88, 207-214.

Brockmann, H. J. & Barnard, C. J. (1979). Kleptoparasitism in birds. *Animal Behaviour*, 27, 487-514.

Broom, M., Luther, R. M. & Ruxton, G.D. (2004). Resistance is useless? Extensions to the game theory of kleptoparasitism. *Bulletin of mathematical biology*, 66, 1645-1658 doi:10.1016/j.bulm.2004.03.009

Broom, M., Luther, R.M., Ruxton, G.D. & Rychtar, J. (2008). A game-theoretic model of kleptoparasitic behaviour in polymorphic populations. *Journal of theoretical biology*, 255, 81-91.

Broom, M. & Ruxton, G.D. (1998). Evolutionarily stable stealing: game theory applied to kleptoparasitism. *Behavioural Ecology*, 9, 397-405.

Broom, M. & Ruxton, G.D. (2003). Evolutionarily stable kleptoparasitism: Consequences of different prey types**.** *Behavioral Ecology*, 14, 23-33. *doi: 10.1093/beheco/14.1.23*

Broom, M. & Rychtár, J. (2007). The evolution of a kleptoparasitic system under adaptive dynamics**.** *Journal of Mathematical Biology*, 54, 151-177. *doi: 10.1007/s00285-006-0005-2*

Broom, M. & Rychtár, J. (2009**).** A game theoretical model of kleptoparasitism with incomplete information. *Journal of Mathematical Biology*, 59, 631-649. *doi: 10.1007/s00285-008-0247-2*

Broom, M, & Rychtar, J. (2013). *Game-theoretical models in biology*. Boca Raton, CRC Press.

Burger, J. (1980). Age differences in foraging black-necked stilts in Texas. *Auk*, 97, 633-636.

Burnham, K.P. & Anderson, D.R. (2001). Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research,* 28, 111–119.

Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003). Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences,* 100, 1781-1786.

Colwell, M.A. (2010). *Shorebird Ecology, Conservation, and Management*. University of California Press, Berkeley, USA.

Darwin, C. (1859). *On the origin of species by means of natural selection*. London. Vintage Books.

Davies, N.B., Krebs, J.R., & West, S.A. (2012). *An introduction to behavioural ecology* (4th ed.). Chichester. Wiley- Blackwell.

Eaton, M.A., Aebischer, N.J., Brown, A.F., Hearn, R., Lock, L., Noble, D.G., Musgrave, A.J., Noble, D.G., Stroud, D., & Gregory, R.D. (2015)**.** Birds of conservation concern 4. *British Birds*, 108, 708-746.

Ens, B.J. & Cayford, J.T. (1996). Feeding with other oystercatchers. In J.D. Goss-Custard (ed). *The Oystercatcher: From Individuals to Populations,* p. 77- 104, Oxford, Oxford University Press.

Giraldeau, L-A. & Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Tree*, 14, 102-106.

Giraldeau, L-A. & Caraco, T. (2000). *Social Foraging Theory*. Princeton. Princeton University Press.

Giraldeau, L-A. & Livoreil, B. (1998). Game theory and social foraging. In L. A. Dugatkin & H. K. Reeve (Eds.), *Game Theory and Animal Behaviour*, p.16-37, New York, Oxford University Press.

Gochfield, M. & Burger, J. (1981). Age-related differences in piracy of Frigatebirds from Laughing gulls. *Condor*, 83, 79-82.

Google (2016). Google earth pro. (Images accessed and downloaded on July 8, 2016) [Computer software].

Grant, P.J. (1982). *Gulls: a guide to identification*. London. T & AD Poyser Ltd.

Hadjichrysanthou, C. & Broom, M. (2012). When should animals share food? Game theory applied to kleptoparasitic populations with food sharing. *Behavioral Ecology*, 23, 977-991. *doi: 10.1093/beheco/ars061*

Hogan-Warburg, A.J. (1966). Social behaviour of the ruff (*Philomachus pugnax*). *Ardea,* 54, 109-229. doi: *http://dx.doi.org/10.5253/arde.v54*

Holmgren, N. (1995). The ideal free distribution of unequal competitors: Predictions from a behavioural-based functional response. *Journal of Animal Ecology*, 64, 197-212.

Hamilton, I.M. (2002). Kleptoparasitism and the distribution of unequal competitors. *Behavioural ecology*, 13, 260-267.

Hamilton, W.D. (1964). The genetical evolution of social behaviour 11, *Journal of theoretical biology,* 7, 17-52.

Hansen, A.J. (1986). Fighting behaviour in bald eagles: A test of game theory. *Ecology*, 67, 787-797.

Hegner, R. H. (1985). Dominance and anti-predator behaviour in blue tits (*Parus cueruleus*). *Animal Behaviour*, 33, 762-768

Hopkins, C.D. & Wiley, R.H. (1972). Food parasitism and competition in two terns. *The Auk,* 89, 583 -594.

King, A.J., Isaac, N.J.B. & Cowlishaw, G. (2009). Ecological, social and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioural Ecology*, 20, 1039-1049.

Leeman, L.W., Colwell, M.A., Leeman, T.S. & Mathis, R.L. (2001). Diets, energy intake, and kleptoparasitism of nonbreeding Long-billed Curlews in a northern California estuary. *Wilson Bulletin,* 113, 194-201.

Luther, R.M. & Broom, M. (2004). Rapid convergence to an equilibrium state in kleptoparasitic populations. *Journal of Mathematical Biology*, 48, 325-339. doi: *10.1007/s00285-003-0237-3*

Madden, B. & Newton, S.F. (2004). Herring Gull *Larus argentatus*. In: Mitchell, P.I., Newton, S.F., Ratcliffe, N. & Dunn, T.E. (eds.). *Seabird Populations of Britain and Ireland*, 242-262, Poyser, London.

Malling Olsen, K. & Larsson, H. (2003). *Gulls of Europe, Asia, and North America*. Chrisopher Helm, London.

Maniscalco, J. M. & Ostrand, W. D. (1997). Seabird behaviors at forage fish schools in Prince William Sound, Alaska. In Forage Fishes in Marine Ecosystems. *Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems*. Alaska Sea Grant College Program Report No. 97-01, p.175-190, University of Alaska Fairbanks, 1997.

Martinez-Abrain, A., Gonzalez-Solis, J., Pedrocchi, V., Genovart, M., Abella, J.C., Ruiz, X., Jiminez, J. & Oro, D. (2003). Kleptoparasitism, disturbance and predation of yellow-legged gulls on Audouin's gulls in three colonies of the western Mediterranean, *Scientia Marina*, 67, 89-94.

Marzluff, J.M., Bowman, R. & Donnelly, R. (2001). *Avian ecology and conservation in an urbanising world*. Kluwer Academic Publishers, Norwell, MA.

MATLAB and Statistics Toolbox Release 2015b. (2015). The MathWorks, Inc., Natick, Massachusetts, United States [computer software].

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge. Cambridge University Press.

Maynard Smith, J., & Parker, G.A. (1976). The logic of asymmetric contests. *Animal Behaviour*, 24, 159-175.

Maynard Smith, J. & Price, G. (1973). The logic of animal conflict. *Nature*, 246, 15-18.

Milinski, M. & Parker, G.A. (1991). Competition for resources. In J.R. Krebs & N.B. Davies (Eds.), *Behavioural Ecology: An evolutionary approach,* p. 137-168, Oxford, Blackwell.

Monaghan, P. & Duncan, N. (1979). Plumage variation in known-age Herring gulls. *British Birds*, 72, 100-103.

Morand-Ferron, J., Giraldeau, L-A. & Lefebvre, L. (2007). Wild Carib grackles play a producer-scrounger game. *Behavioural Ecology*, 916-921, doi:10.1093/beheco/arm058

Nash, J. (1951). Non-cooperative games. *The Annals of Mathematics,* 54, 286–95. doi:10.2307/1969529

Page, S.E. (2008). *The Difference: How the power of diversity creates better groups, firms, schools and societies.* Princeton University Press, Princeton, NJ.

Polak, B. (2008). Mixed strategies in baseball, dating and paying your taxes. Retrieved from https://www.youtube.com/watch?v=9b2AMWwMToc&list=PL6EF60E1027E1A10B&index=10

Pons, J.-M., Hassanin, A. & Crochet, P.-A. (2005). Phylogenetic relationships within the *Laridae (Charadriiformes:Aves)* inferred from mitochondrial markers. *Molecular phylogenetics and evolution*, 37, 686-699.

Proctor, N.S. & Lynch, P.J. (1993). *Manual of ornithology: Avian structure and function*. New Haven, Yale.

Quintana, F. & Yorio, P. (1999). Kleptoparasitism by kelp gulls and royal and cayenne terns at Punta Leon, Argentina. *Journal of Field Ornithology*, 337-342.

R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/

Rands, S. A. (2011). The effects of dominance on leadership and energetic gain: a dynamic game between pairs of social foragers. *PLoS Computational Biology*, 7(10), doi: [e1002252].10.1371/journal.pcbi.1002252

Railsback, S.F. & Grimm, V. (2012). *Agent-based and Individual-based Modelling: A practical introduction*. Oxford. Princeton University Press.

Ranta, E., Peuhkuri, N., Laurila, A., Rita, H., & Metcalfe, N.B. (1996). Producers, scroungers and foraging group structure. Animal Behaviour, 51, 171-175.

Reader, S.M. & Laland, K.N. (2003). Animal innovation: An introduction. In S.M. Reader & K.N. Laland (Eds.), *Animal innovation* (pp.3-35). Oxford, Oxford University Press.

Reid, J.B. 2004. Great Black-backed Gull *Larus marinus*. In: Mitchell, P.I., Newton, S.F., Ratcliffe, N. and Dunn, T.E. (eds.) 2004. *Seabird Populations of Britain and Ireland*, 263-276, Poyser, London.

Rock, P. (2005). Urban gulls: problems and solutions, *British Birds*, 98, 338-355.

Ruxton, G.D. & Moody, A.L. (1997). The ideal free distibution with kleptoparasitism. *Journal of theoretical biology*, 186, 449-458.

Schneider, K.J. (1984). Dominance, predation and optimal foraging in white-throated sparrow flocks. *Ecology*, 65, 1820-1827.

Schroeder, J., Nakagawa, S., & Hinsch, M. (2011). Behavioural ecology is not an endangered discipline. *Trends in Ecology and Evolution*, 26, 320.

Scott, P., Duncan, P. & Green, J.A. (2014). Food preferences of the black-headed gull *Chroicocephalus ridibundus* differs along a rural-urban gradient. *Bird Study*, doi: 10.1080/00063657.2014.984655

Shoham, Y. & Leyton-Brown, K. (2009). *Multiagent Systems: Algorithmic, game-theoretical and logical foundations*. Cambridge. Cambridge University Press.

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P. & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Science*, 102, 5460–5465.

Sol, D., Bacher, S., Reader, S.M. & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *American Naturalist,* 172, 63–71.

Spaniel, W. (2011). *Game theory 101*. Create Space Independent Publishing Platform. ISBN-10: 1492728152

Stearns, S. C. & Hoekstra, R.F. (2005). *Evolution: An introduction (2nd Ed.).* Oxford. Oxford University Press

Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory*. Princeton. Princeton University Press.

Sutherland, W. J. (1983). Aggregation and the ideal free distribution. *Journal of Animal Ecology*, 52, 3, 821-828.

Svensson, L., Mullarney, K. & Zetterstrom, D. (2009). *Collins Bird Guide (2nd Ed).* Harper Collins, London.

Thompson, D.B.A. (1986). The economics of kleptoparasitism: optimal foraging host and prey selection by gulls. *Animal Behaviour*, 34, 1189-1205.

Tinbergen, N. (1953). *The Herring Gull's World*. London. Collins.

Van Rhijn, J.G. (1973). Behavioural dimorphism in male ruffs (*Philomahcus pugnax*). *Behaviour*, 47, 153-229.

Verbeek, N.A.M. (1977a). Comparative feeding behaviour of immature and adult herring gulls. *The Wilson Bulletin*, 89, 415-421.

Verbeek, N. A. M. (1977b). Comparative feeding ecology of Herring gulls (*Larus argentatus*) and Lesser Black-backed gulls (*Larus fuscus*). *Ardea*, 65, 25-42.

Vollrath, F. (1984). Kleptobiotic interactions in vertebrates. In C.J. Barnard (Ed.), *Producers and Scroungers: Strategies of exploitation and parasitism*, p. 61-94, Beckenham, Croom Helm.

Waite, T.A. & Field, K.L. (2007). Foraging with others: Games social foragers play. In D.W. Stephens, J.S. Brown, & R.C. Ydenberg (Eds.), *Foraging: behaviour and ecology*, p.331-362, London. University of Chicago Press.

White, E.P., Ernest, S.K.M., Kerkoff, A.J., & Enquist, B.J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, 22, 323-330.

Why are there so many seagulls in cities? (2012). Retrieved November 16, 2016, from http://www.bbc.co.uk/news/magazine-19490866

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.

Wolfram Alpha LLC. (2016). Wolfram|Alpha. http://www.wolframalpha.com (access November 11, 2016) [computer software].

Ydenberg, R.C., Brown, J.S., & Stephens, D.W. (2007). Foraging: An overview. In D.W. Stephens, J.S. Brown, & R.C. Ydenberg (Eds.), *Foraging: behaviour and ecology*, p. 1-28, London, University of Chicago Press.

Ydenberg, R.C. (2010). Decision theory. In D.F. Westneat C.W. Fox (Eds.). *Evolutionary behavioural ecology*, p.131-147, New York. Oxford University Press.

Zeileis, A., Kleiber, C. & Jackman, S. (2008). Regression models for count data in R. *Journal of statistical software*, 27, 1-23.

Appendix A – The Hawk/ Dove Model (Maynard Smith, 1982)

The Hawk/ Dove model was the foundational model in evolutionary game theory. The basic conceit is that two animals of the same species are going to fight over a resource, this resource could be territories, mates, or a food item. The resource has a value (v), so, the fitness of the winner will increase by this amount following the fight. The competing animals have only two strategies available to them: *Hawk* or *Dove*.

Hawk is an aggressive strategy in which, when an animal encounters an opponent and the resource, it escalates and continues to fight until it wins the resource or is injured and cannot continue fighting.

Dove is a passive strategy of bluff in which the animal displays like it is challenging for the resource, but if the opponent escalates the animal backs off immediately, and if the opponent does not escalate the resource is shared between the two opponents after they have finished their ritualised mutual displays.

If two Hawks encounter each other one or both are going to be injured. Injury will reduce fitness by a certain cost (c). So using a Hawk strategy has costs and benefits in that being aggressive can help the animal to acquire resources but if the opponent faced is also a Hawk then injury costs are likely to be incurred. In the foundational model the risk of injury when a Hawk faces a Hawk is set at 50%, so the payoff for a Hawk encountering other Hawks is half of the benefit minus the costs averaged over all encounters $\frac{1}{2}(v-c)$.

A Dove will surrender the resource if it encounters a Hawk, so the payoff for a Dove against a Hawk is zero, it gains no fitness but also incurs no injury costs. The payoff to the Hawk when it encounters a Dove is the full value of the resource or v.

When a Dove meets another Dove they share the resource so the payoff is half the resource value $\frac{1}{2}v$.

These payoffs are summarised in Table A1:

Table A1. Payoff matrix for the Hawk/Dove game.

	Hawk	**Dove**
Hawk	$\frac{v-c}{2}; \frac{v-c}{2}$	$v; 0$
Dove	$0; v$	$\frac{v}{2}; \frac{v}{2}$

Resource = v $(v > 0)$, Cost of fighting = c $(c > 0)$

What is the Evolutionarily Stable Strategy (ESS) for the Hawk/ Dove game?

For a strategy to be an ESS (see section 1.2 and Appendix B) it must be the case that if every member of the population adopts a particular strategy the fitness of a typical member of the population must be greater than the fitness of an animal playing an alternative or mutant strategy.

Pure Strategies:

Dove is not an ESS because a population of Doves can be invaded by a Hawk mutant - $(Dove, Dove)\frac{v}{2} < v(Hawk, Dove)$.

Hawk is an ESS if the payoff for an encounter is greater than the cost of the encounter. So, if all the population are Hawks it will be evolutionarily stable if $v > c$.

Mixed Strategies:

If the cost of injury is very high and $v < c$ then we should expect to see mixed strategies (see appendix B).

Consider a population of all Hawks, if $v < c$ then a mutant Dove will have a payoff of zero against its Hawk opponents, in other words its fitness will remain unchanged. However, when $v < c$ the payoff for Hawks against Hawks $\frac{1}{2}(v - c)$ will be a negative number and therefore less than zero.

In a population of all Doves when $v < c$ a Hawk still wins the resource with no injury costs so it will have high fitness because it only ever encounters Doves.

From either of these starting points (all Hawks or all Doves), when $v < c$ the population will evolve to a stable intermediate frequency of the two strategies where the payoffs for both strategies are equal. The proportion of Hawks to Doves in this ESS will depend on the actual values of v and c.

If $v < c$ then the proportion of Hawks in the ESS population mix will be given by $\frac{v}{c}$. As v increases there will be more Hawks in the ESS population, when c increases the ESS will contain more Doves.

Appendix B – Formal definitions - Nash Equilibruim (NE) and Evolutionarily Stable Strategy (ESS). Following Shoham & Leyton-Brown (2009) and Polak (2008).

Game theory analyses interdependent strategic interactions involving the following components:

- *Players* who make strategic decisions.
- A set of *strategies* the players are able to take.
- *Payoffs* the players receive for the given strategy they choose.

The name game theory, and the use of terminology such as players, is misleading as it can convey the impression that game theoretic situations are trivial. This is unfortunate and inaccurate as the situations analysed using game theory include any interactions where the outcome is influenced by the actions the various parties involved take.

Game theoretic solution concepts find a stable *equilibrium* where players choose the action or strategy that gives each player their highest payoff given the actions chosen by the other players. This is called their *best response* (BR). If all players make their BR then the population/ interaction will be at a stable equilibrium because no individual can profit by changing to a different action.

In most cases players are not going to know what actions other players will take but given repeated interactions (rounds of the game) they should learn the rules and learn their BR, thus the game will evolve towards an equilibrium.

Players can play a *pure strategy* where only one action is played with positive probability, or they can play a *mixed strategy* where they change between, or randomise between, different actions with given probabilities. In formal definitions the actions used in pure strategies are signified by the letter a. To differentiate them from pure strategies, in a mixed strategy the various different actions the players might take are called *strategy sets* and are represented in formal definitions by the letter s.

Pure strategy – Only one action (a) is played with positive probability.

Mixed strategy – Multiple actions (s) are played by each player with positive probability.

A *Nash Equilibrium* (NE) (Nash, 1951) is a core solution concept in game theory. A NE is a set of strategies, one for each player, such that each player is making their BR and no player has incentive to change their strategy given what the other players are doing (Spaniel, 2011).

Formal definitions of BR and pure and mixed strategy NE are provided below:

Pure Strategy – BR and NE:

BR – To be a BR the utility (u_i) of playing action a_i^* has to be as great as any other action that might be chosen whatever actions the other players use. Where u_i is a utility payoff signified by a generic index i from a set of possible utility payoffs indexed from a to n $(u_a, u_b, \dots, u_n)$, and a_i^* denotes an

action a^* chosen by player i over alternative action a in response to the actions taken by the other players a_{-i}. Formally this is captured by the inequality:

$a_i^* \in BR(a_{-i}) \; iff \; \forall \, a_i \in A_i, u_i(a_i^*, a_{-i}) \geq u_i(a_i, a_{-i})$

(Shoham & Leyton-Brown, 2009).

NE – A NE is a set of actions (a), one for each player, such that each is a BR to the others, so no player has an incentive to change strategy. Formally:

$a = (a_1, \ldots, a_n)$ is a pure strategy NE $iff \; \forall i, a_i \in BR\,(a_{-i})$

(Shoham & Leyton-Brown, 2009).

Mixed Strategy – BR and NE:

For mixed strategies we have to replace the individual actions (a) used in the pure strategy definition above, with strategy sets (s).

BR – In the set of all possible strategies available to a player the utility (u_i) for playing strategy set s_i^* when everyone else plays the strategy profile s_{-i} to be a BR must be equal to or greater than playing the other strategies s_i available to that player. Formally:

$s_i^* \in BR\,(S_{-i}) \; iff \; \forall s_i \in S_i, u_i\,(s_i^*, s_{-i}) \geq u_i\,(s_i, s_{-i})$

(Shoham & Leyton-Brown, 2009).

NE – Strategy profile s is a NE if all agents are playing their BR (there may be more than one). Formally:

$s = (s_1, \ldots, s_n) is \; a \; NE \; iff \; \forall i, s_i \in BR\,(s_{-i})$

(Shoham & Leyton-Brown, 2009).

Not all pure strategy games have a NE, but the above definition of a mixed strategy NE gives us the following theorem 'Every finite game has a Nash Equilibrium' (Nash, 1951). This means that any game which has a finite number of players, actions, and payoffs has at least one NE, if not in pure strategies then in mixed strategies. So, if a player knew what actions other players would take there is at least one action or strategy set that player could use that will give them their greatest payoff given what the other players are doing (Shoham & Leyton-Brown, 2009).

Evolutionary Stability

Analyses in game theory make the assumption of rationality (Maynard Smith, 1982), that is, with sufficient knowledge of the game individuals will make rational decisions to maximise their payoffs. In evolutionary game theory the rational agent is assumed to be natural selection (Darwin, 1859) and the payoffs are measured in terms of fitness gains and losses. Evolutionary game theory analyses the

fitness of different phenotypes as a consequence of their frequency in the population. Phenotypic traits that have a high relative fitness will increase in prevalence in the population and those that do less well will decrease, this is the basis of natural selection.

The solution concept in evolutionary game theory is the *evolutionarily stable strategy* (ESS). Strategy in this definition refers to behavioural phenotypes, specifically how an individual will behave in a given situation where it interacts with other individuals or organisms.

An ESS is defined as a strategy (behaviour) such that "if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection" (Maynard Smith, 1982, p.10). For ease and tractability of analysis models of evolutionary stability often make the simplifying assumptions that the population is infinite, reproduces asexually, and that the strategic interactions are symmetric contests between two players (Maynard Smith, 1982). Symmetric meaning that both players have the same profile of actions available to them. This makes the definition of ESS tighter than that of NE given above. As a result, although both NE and ESS are solution concepts that deal with equilibria or stable states, it can be shown that all ESS are also NE, but not all NE are ESS (Polak, 2008). ESS's were first formally defined by Maynard Smith and Price (1973), the definitions outlined below are variations but equivalent definitions to Maynard Smith and Price (1973) as outlined by Polak (2008).

As with NE, ESS's can be defined for both pure and mixed strategies. Evolutionarily stable pure strategies can be argued to correspond to situations in nature which are monomorphic, where only one phenotype exists. Stable mixed strategies correspond to situations in nature which are described as polymorphic, where multiple phenotypes exist (Polak, 2008).

Formal definitions of pure and mixed strategy ESS are outlined below:

Pure Strategy – ESS:

Strategy $\hat{s}$ is an ESS if, against all possible mutations s', the payoff of $\hat{s}$ against the mixed population is bigger than the payoff of s'against the mixed population. Mixed here means the population consisting of the strategy of interest and the mutant strategy trying to invade. Another way to state the above is, for $\hat{s}$ to be evolutionarily stable is has to do at least as well against itself as against s' and better against s' than s' does against itself. Formally:

In a symmetric two player game, a strategy $\hat{s}$ is an ESS in pure strategies if:

a) $(\hat{s}, \hat{s})$ is a symmetric NE. ie. $u\,(\hat{s}, \hat{s}) \geq u\,(s', \hat{s})\ for\ all\ s'$ and:
b) $If\ u\,(\hat{s}, \hat{s}) = u\,(s', \hat{s}), then\ u\,(\hat{s}, s')\ > u\,(s', s')$.

(Polak, 2008).

Mixed Strategy – ESS:

When using a mixed strategy an individual is randomising with positive probability between two or more behaviours, as such there is a given probability mix of those behaviours – the frequency with

which each behaviour is used – at an equilibrium that individual is indifferent between which behaviour is used as, in equilibrium proportions, the payoffs are equal across behaviours. So, unlike pure strategies, there is no single strategy or behaviour that is strictly the best to use. This is an essential feature of mixed strategies generally but is an important part of the definition of a mixed ESS. As no single behaviour is strictly the best to use a mixed ESS cannot also be a strict (pure strategy) NE.

To define a mixed strategy ESS the letter p is used to signify that the phenotypes of interest are now profiles of strategies, in contrast to playing a single strategy s used to formalise pure strategies above. For strategy profile $\hat{p}$ to be a mixed strategy ESS it must be a symmetric NE that is not a strict NE, and $\hat{p}$ does at least as well against itself as the strategy profile p', and does better against p' than p' does against itself. Formally, this can be stated as:

In a two player symmetric game, a strategy profile $\hat{p}$ is a mixed strategy ESS if:

a) $(\hat{p}, \hat{p})\ is\ a\ symmetric\ NE$ and:
b) $(\hat{p}, \hat{p})\ is\ NOT\ a\ strict\ NE\ (ie. there\ is\ a\ p' \neq \hat{p})\ with\ u\ (\hat{p}, \hat{p}) = u\ (p', \hat{p}) then\ u\ (\hat{p}, p') > u\ (p', p')$.

(Polak, 2008).

A mixed ESS can be validly interpreted in two ways. First, an individual is randomising between different strategies. Second, the populations consists of two or more types in the stable proportions. A consequence of the conditions for a mixed strategy ESS stated above is that a competitive interaction can have multiple strategy profiles that are evolutionarily stable. These ESS's need not all be equally good, but they are the BR given what other players are doing.

Appendix C – Frequency-dependent selection

Frequency-dependent selection describes an evolutionary process where the fitness of a phenotype, genotype or trait is dependent on its frequency relative to other such phenotypes, genotypes or traits present in the population.

Frequency-dependent selection operates in two main ways:

- Positive frequency-dependence: This occurs when the fitness of a phenotype increases as it becomes more common. Aposematism is a good example of this seen in nature. The bright warning colouration seen among many species often signals the toxic and distasteful nature of those organisms that acts as a warning to potential predators. The benefits of this warning colouration to deter predators are only fully realised when the signal is sufficiently prevalent in the population. The more individuals of a species that carry the trait in a population then the quicker predators will learn the association between the bright colours and the unpalatable taste of the organisms carrying it.
- Negative frequency-dependence: The fitness of a phenotype decreases as that phenotype becomes more prevalent in the population. This type of frequency-dependence is likely much more common than positive frequency-dependence. Numerous examples are found in nature that relate to competitive interactions between individuals. For example, in botany it has been shown that certain plant species will have higher fitness when they are surrounded by unrelated species rather than clustered with members of their own species. When clustered in groups surrounded by plants of their own type that have similar resource requirements, competition is higher and their overall fitness is reduced (Stearns & Hoekstra, 2005).

In behavioural ecology negative frequency-dependence often maintains multiple behavioural strategies within a species or population. In social foraging theory, P-S models provide perhaps the best example of negative frequency-dependence as the success of a behaviour depends on what others in the population are doing. An example is discussed below.

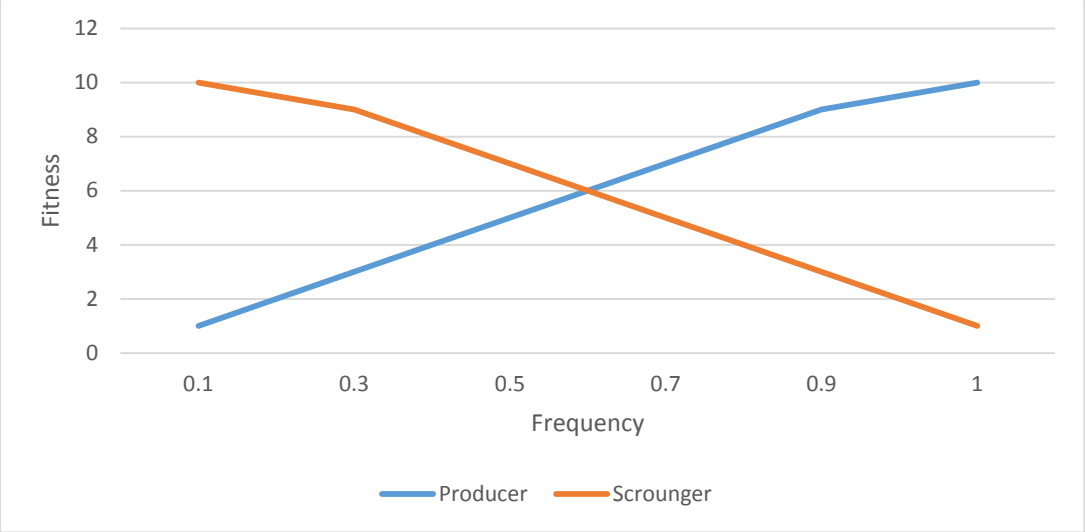


Figure C1. Frequency Dependent Selection. The fitness of each strategy (Producer or Scrounger) changes as a consequence of its prevalence in relation to the other strategy. For example, if scroungers are prevalent in the population the fitness of both producers and scrounger is low as there will be multiple individuals trying to steal from a small number of producers. Conversely if producers are prevalent in the population and there are few scroungers both strategies will have higher fitness as there are numerous individuals finding new food items from whom the small group of scroungers can try to steal. Note that the intersection point of the producer and scrounger strategies is the evolutionarily stable strategy (ESS).

Figure C1 shows how the solution to negative frequency-dependent P-S competitions can be readily illustrated using linear models. For example, consider a population of n individuals that, for ease of analysis, are haploid and reproduce asexually. The individuals in this population have two foraging strategies that they can utilise. They can produce or they can scrounge. For the purpose of illustration let us also assume that they specialise in one of these two strategies. When the population consists almost entirely of producers, and scroungers are rare, scroungers will do better than producers as each scrounger will readily encounter producers from whom they can steal. Scroungers will therefore have higher fitness than producers as they have not had to pay the costs of searching for and finding their own prey items. This higher fitness will be converted to greater reproductive success and in the next generation the prevalence of scroungers will increase in the population. If this continues generation on generation for some time, with the number of scroungers increasing and the number of producers declining, an equilibrium point will eventually be reached when the frequency of each tactic is such that the two behaviours will have equal payoffs. This is the point where the two lines intersect in figure C1 and is the evolutionarily stable strategy (ESS) (See also section 1.4 and Appendix B) for this P-S model. If the prevalence of scrounging were to continue increasing beyond this point its fitness would start to decrease relative to the producer strategy as there would be many scroungers competing to steal from few producers. Logically, a population of scroungers needs some producers otherwise there are no individuals finding food from whom to steal (Giraldeau & Livoreil, 1998). As the number of scrounger in the population declines over time relative to the number of producers it once again becomes a profitable strategy to engage in scrounging when the strategy is sufficiently rare.

When populations do not settle at the ESS the result can be this constant cycling of the two strategies as their prevalence increases and decreases as a result of negative frequency-dependent selection.

Appendix D – Area calculations for Billingsgate and Brancaster study sites

Figure D1. Billingsgate study area. The study area (Trader's Car Park) at Billingsgate Market demarcated by the black rectangle. The measurements of the study area encompassed within the black rectangle shown below were obtained using the measurement tool on Google Earth Pro. Image obtained from Google Earth Pro 21/10/15.

Black rectangle measurement:

Length x height = area

130m x 80m = 10,400$m^2 \approx 0.0104 km^2$

Figure D2. Brancaster study area. The study area at Brancaster beach consisted of the areas encompassed by the black rectangle and the red triangle. The measurements of the study area encompassed within these two shapes were obtained using the measurement tool on Google Earth Pro. Image obtained from Google maps 10/09/15.

Black rectangle measurement:

Length x height = area

1800m x 800m = 1,440,000m^2

Red triangle measurement:

0.5 x base x height = area

0.5 x 400m x 800m = 160,000m^2

Total study area:

Black rectangle + Red triangle = Total study area

1,440,000 + 160,000 = 1,600,000$m^2 \approx 1.6km^2$

Appendix E – Examples of plumages for different age categories of Herring gull (*Larus argentatus*)

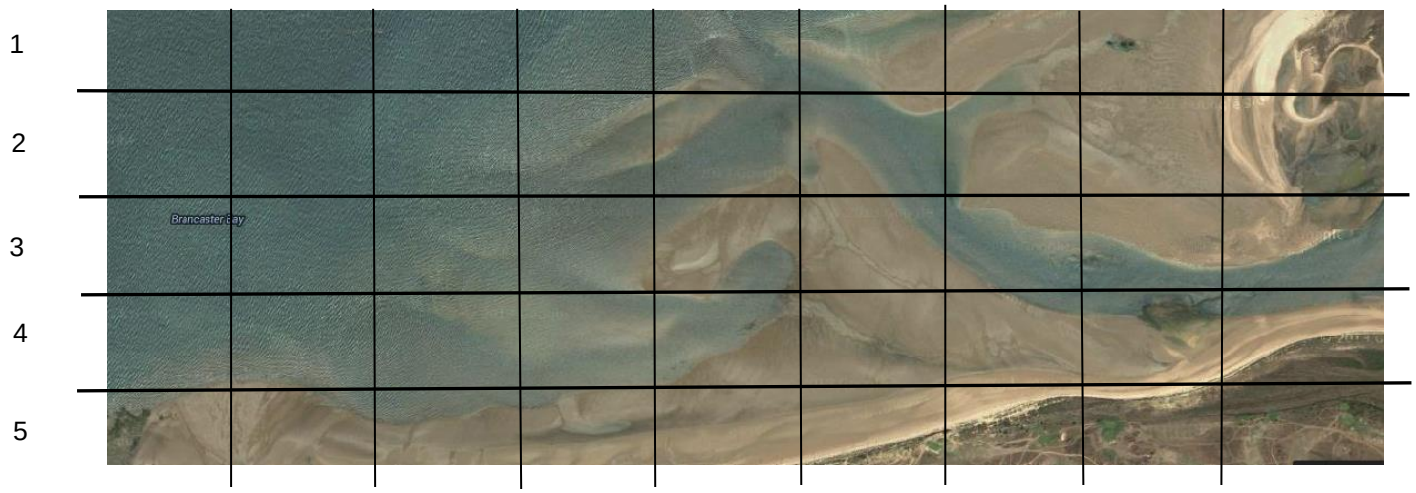
Figure E1. Juvenile herring gull. Plumage entirely brown with dark eye and bill colouration. Photograph obtained from Wikimedia creative commons.

Figure E2. Sub-adult herring gull. Plumage is a mix of brown juvenile feathers and silver feathers typical of adult plumage on the mantel. Eye and bill both beginning to lighten in colour. Photograph by © Hans Hillewaert /, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=2984877

Figure E3. Adult herring gull. Adult plumage typified by silver primaries, secondaries and covert feathers. White feathers on head and body, with a light coloured eye and bright yellow colouration with a red spot on the bill. Photograph obtained from Wikimedia creative commons.

Appendix F – Patch Datasheet Brancaster study site

Diagram of Site:

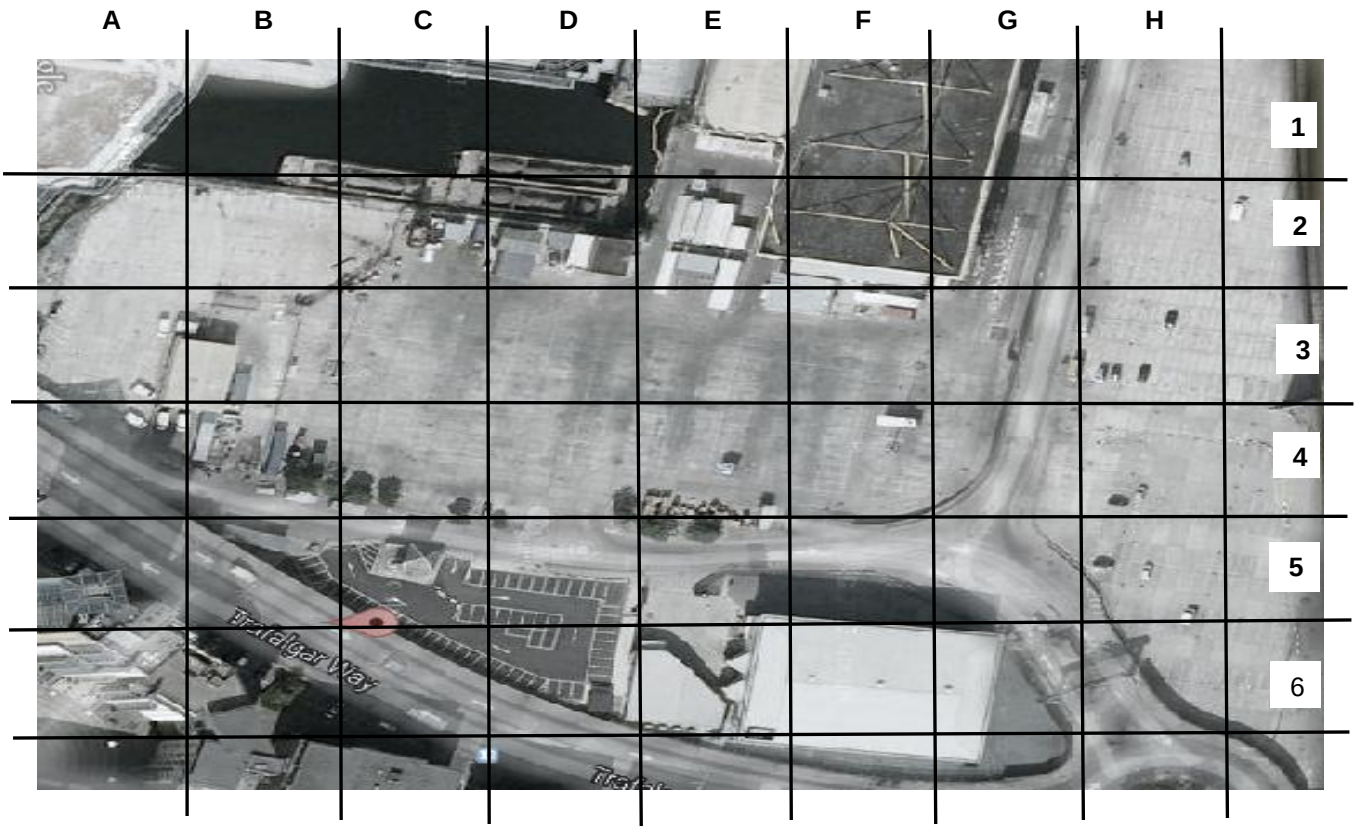


Date: **Start:** **Finish:** **Observer:**

Recording	Time	Duration	Headcount	Species	Camera	Notes

Appendix G – Patch Datasheet Billingsgate study site

Diagram of site:



Date: **Time Start:** **Finish:** **Observer:**

Patch No.	Time	Depletion Time	Food	Headcount @ Patch	Species	Camera

Appendix H – Datasheet used for the field experiment conducted at Billingsgate

Date: **Location:** **Start:** **Finish:**

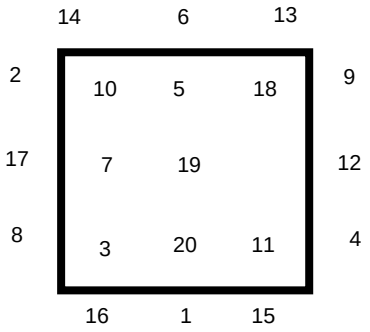
Trap Location (grid square): **Headcount:** Total: Species:

Video:

Food items provisioned (ranked highest to lowest calories):

No.	Food	Calories	No.	Food	Calories
1	1 Slice of bread	100	11	¼ Slice of bread	25
2	½ Can sardines	86.5	12	1/9 Slice of bread	11.1
3	½ Can sardines	86.5	13	1/9 Slice of bread	11.1
4	White fish fillet	61	14	1/9 Slice of bread	11.1
5	White fish fillet	61	15	1/9 Slice of bread	11.1
6	½ Slice of bread	50	16	1/9 Slice of bread	11.1
7	½ Slice of bread	50	17	1/9 Slice of bread	11.1
8	¼ Slice of bread	25	18	1/9 Slice of bread	11.1
9	¼ Slice of bread	25	19	1/9 Slice of bread	11.1
10	¼ Slice of bread	25	20	1/9 Slice of bread	11.1

Diagram (Food Position by item number):



Black square shows an aerial view of the enclosure depicting the location of different size and value food item.

Depletion of food items:

No.	Food	Calories	In/Out	No.	Food	Calories	In/Out

Pirate				Victim		Aerial Pursuit	No. of Pursuers	Food Item No.
Species	Age	Type	Success	Species	Age			

Appendix I – Solutions to system of dynamical equations describing equilibrium densities in the Billingsgate population

I.1 – Solving the system of linear first order ODE's:

First solving for C (Stealth kleptoparasites):

$$\frac{dC}{dt} = p_2 p_4 v_h SH - \frac{2}{t_c} C = 0 \quad (1)$$

$$p_2 p_4 v_h SH - \frac{2}{t_c} C = 0 \quad (2)$$

$$\frac{2}{t_c} C = p_2 p_4 v_h SH \quad (3)$$

$$C = \frac{p_2 p_4 v_h SH}{2/t_c} \quad (4)$$

$$C = \frac{p_2 p_4 v_h SH}{1} \times \frac{t_c}{2} \quad (5)$$

$$\boldsymbol{C = \frac{p_2 p_4 t_c v_h SH}{2}} \quad (6)$$

Solving for R (Resistors):

$$\frac{dR}{dt} = p_2 p_4 v_h SH - \frac{2}{t_c} R \quad (7)$$

$$p_2 p_4 v_h SH - \frac{2}{t_c} R = 0 \quad (8)$$

$$\frac{2}{t_c} R = p_2 p_4 v_h SH \quad (9)$$

$$R = \frac{p_2 p_4 v_h SH}{2/t_c} \quad (10)$$

$$R = \frac{p_2 p_4 v_h SH}{1} \times \frac{t_c}{2} \quad (11)$$

$$\boldsymbol{R = \frac{p_2 p_4 t_c v_h SH}{2}} \quad (12)$$

Solving for A (Aggressive kleptoparasites):

$$\frac{dA}{dt} = p_1 p_3 v_h SH - \frac{2}{t_a} A = 0 \quad (13)$$

$$p_1 p_3 v_h SH - \frac{2}{t_a} A = 0 \quad (14)$$

$$\frac{2}{t_a} A = p_1 p_3 v_h SH \quad (15)$$

$$A = \frac{p_1 p_3 v_h SH}{2/t_a} \quad (16)$$

$$A = \frac{p_1 p_3 v_h SH}{1} \times \frac{t_a}{2} \quad (17)$$

$$\boldsymbol{A = \frac{p_1 p_3 t_a v_h SH}{2}} \quad (18)$$

Solving for D (Defenders):

$$\frac{dD}{dt} = p_1 p_3 v_h SH - \frac{2}{t_a} D = 0 \quad (19)$$

$$p_1 p_3 v_h SH - \frac{2}{t_a} D = 0 \quad (20)$$

$$\frac{2}{t_a} D = p_1 p_3 v_h SH \quad (21)$$

$$D = \frac{p_1 p_3 v_h SH}{2/t_a} \quad (22)$$

$$D = \frac{p_1 p_3 v_h SH}{1} \times \frac{t_a}{2} \quad (23)$$

$$\boldsymbol{A = \frac{p_1 p_3 t_a v_h SH}{2}} \quad (24)$$

Solving for S (searchers) and substituting solutions for C, R, A and D:

$$\frac{dS}{dt} = \frac{1}{t_h}H + \frac{2}{t_c}(1-\beta)C + \frac{2}{t_c}\beta R + \frac{2}{t_a}(1-\alpha)A + \frac{2}{t_a}\alpha D - v_f f S - p_1 p_3 v_h SH - p_2 p_4 v_h SH = 0 \quad (25)$$

$$\frac{H}{t_h} + \frac{2}{t_c}(1-\beta)\left(\frac{p_2 p_4 t_c v_h SH}{2}\right) + \frac{2}{t_c}\beta\left(\frac{p_2 p_4 t_c v_h SH}{2}\right) + \frac{2}{t_a}(1-\alpha)\left(\frac{p_1 p_3 t_a v_h SH}{2}\right) + \frac{2}{t_a}\alpha\left(\frac{p_1 p_3 t_a v_h SH}{2}\right) - v_f f S - p_1 p_3 v_h SH - p_2 p_4 v_h SH = 0 \quad (26)$$

$$\frac{H}{t_h} + \frac{2}{t_c}\frac{p_2 p_4 t_c v_h SH}{2} - \frac{2}{t_c}\frac{p_2 p_4 t_c v_h SH}{2}\beta + \frac{2}{t_c}\frac{p_2 p_4 t_c v_h SH}{2}\beta + \frac{2}{t_a}\frac{p_1 p_3 t_a v_h SH}{2} - \frac{2}{t_a}\frac{p_1 p_3 t_a v_h SH}{2}\alpha + \frac{2}{t_a}\frac{p_1 p_3 t_a v_h SH}{2}\alpha - v_f f S - p_1 p_3 v_h SH - p_2 p_4 v_h SH = 0 \quad (27)$$

$$\frac{H}{t_h} + \frac{2}{t_c}\frac{p_2 p_4 t_c v_h SH}{2} + \frac{2}{t_a}\frac{p_1 p_3 t_a v_h SH}{2} - v_f f S - p_1 p_3 v_h SH - p_2 p_4 v_h SH = 0 \quad (28)$$

$$\frac{H}{t_h} - v_f f S = 0 \quad (29)$$

$$v_f f S = \frac{H}{t_h} \quad (30)$$

$$S = \frac{H/t_h}{v_f f} \quad (31)$$

$$S = \frac{H}{t_h} \times \frac{1}{v_f f} \quad (32)$$

$$\boldsymbol{S = \frac{H}{t_h v_f f}} \quad (33)$$

Substituting the solution from equation 33 for S in the solutions for C, R, A and D (equations: 6, 12, 18 and 24):

$$C = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} \quad (34)$$

$$R = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} \tag{35}$$

$$A = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \tag{36}$$

$$D = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \tag{37}$$

Solving for H using the population equation:

$$P = S + H + A + D + C + R \tag{38}$$

$$P = \frac{H}{t_h v_f f} + H + \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \tag{39}$$

$$P = \frac{H}{t_h v_f f} + H + \frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \tag{40}$$

$$P = H + \frac{H + p_2 p_4 t_c v_h H^2 + p_1 p_3 t_a v_h H^2}{t_h v_f f} \tag{41}$$

$$t_h v_f f P = t_h v_f f H + H + p_2 p_4 t_c v_h H^2 + p_1 p_3 t_a v_h H^2 \tag{42}$$

$$t_h v_f f P - p_2 p_4 t_c v_h H^2 - p_1 p_3 t_a v_h H^2 = t_h v_f f H + H \tag{43}$$

$$\boldsymbol{H = -(p_1 p_3 t_a + p_2 p_4 t_c) v_h H^2 - \left(1 + t_h v_f f\right) H + t_h v_f f P} \tag{44}$$

I.2 – Testing the system using data from Billingsgate:

Table I.1. Known parameters for Billingsgate.

Parameter	Value
H	2.52
S	8.52
C	0.18
R	0.18
A	0.3
D	0.3
P	12
$\boldsymbol{\alpha}$	0.79
$\boldsymbol{\beta}$	0.71
$\boldsymbol{p_1}$	0.38
$\boldsymbol{p_2}$	0.23
$\boldsymbol{p_3}$	0.35
$\boldsymbol{p_4}$	0.64
$\boldsymbol{v_f f}$	0.71
$\boldsymbol{v_h}$	0.83
$\boldsymbol{x}$	0.63

Table I.2. Unknown parameter values for Billingsgate.

Parameter	Value
$\boldsymbol{t_h}$	Investigated numerically
$\boldsymbol{t_c}$	Investigated numerically
$\boldsymbol{t_a}$	Investigated numerically

Substituting the values from Table ?.1 into the equilibrium equations and solving:

$$S = \frac{H}{t_h v_f f} \tag{45}$$

$$8.52 = \frac{2.52}{t_h \times 0.71} \tag{46}$$

$$\boldsymbol{t_h = 0.42} \tag{47}$$

$$C \ \& \ R = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} \tag{48}$$

$$0.18 = \frac{1}{2}\frac{0.23 \times 0.64 \times t_c \times 0.83 \times 2.52^2}{0.42 \times 0.71} \tag{49}$$

$$\frac{t_c \times 0.7758176}{0.5964} = 0.18 \tag{50}$$

$$t_c = \frac{0.107352}{0.775816} \tag{51}$$

$$\boldsymbol{t_c = 0.138 \approx 0.14} \tag{52}$$

$$A\ \&\ D = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} \tag{53}$$

$$0.3 = \frac{1}{2}\frac{0.38\times0.35\times t_a\times0.83\times2.52^2}{0.42\times0.71} \tag{54}$$

$$\frac{t_a \times 0.7009765}{0.5964} = 0.3 \tag{55}$$

$$t_a = \frac{0.17892}{0.7009765} \tag{56}$$

$$\boldsymbol{t_a = 0.255 \approx 0.26} \tag{57}$$

Appendix J – Justifying the treatment of repeatedly handled food items

Consider the situation where a handler is attacked using ST kleptoparasitism by a mutant handler in a population that does not use kleptoparasitism. The conditions when it is advantageous for a handler to resist are given by inequality 1 which simplifies to inequality 2:

$$\frac{t_c}{2} + \beta x\left(\frac{1}{v_f f}\right) < \frac{1}{v_f f} \qquad (1)$$

$$v_f f < \frac{2(1-\beta x)}{t_c} \qquad (2)$$

Consider now a situation where a handler is attacked using ST kleptoparasitism by a mutant handler in a population that does not use kleptoparasitism and successfully resists the attack, it obtains a payoff of $(1-\beta)$. That handler is then attacked again using stealth and on this occasion loses. It now obtains a payoff of the quantity it retains from resisting, despite the loss, multiplied by the time required to search for and find another food item: $(1-x)\beta(\frac{1}{v_f f})$. On this second occasion the conditions when it is advantageous for a handler to resist despite the prior handling of the item are given by inequality 3. The condition in inequality 3 simplifies to the same expression as inequality 2, as shown by the steps in inequalities 3, 4, 5, 6, 7, 8 and 9.

$$1-\beta+(1-x)\beta\left(\frac{1}{v_f f}\right)+t_h > \frac{t_c}{2}+(1-\beta)t_h+\beta(1-x)t_h \qquad (3)$$

$$1-\beta x\left(\frac{1}{v_f f}+t_h\right) > \frac{t_c}{2}+(1-\beta x)t_h \qquad (4)$$

$$\frac{1-\beta x}{v_f f}+t_h(1-\beta x) > \frac{t_c}{2}+(1-\beta x)t_h \qquad (5)$$

$$\frac{1-\beta x}{v_f f} > \frac{t_c}{2} \qquad (6)$$

$$\frac{2(1-\beta x)}{v_f f} > t_c \qquad (7)$$

$$2(1-\beta x) > t_c v_f f \qquad (8)$$

$$\frac{2(1-\beta x)}{t_c} > v_f f \qquad (9)$$

This derivation indicates that the conditions when it is advantageous to resist are the same even if the contested item has previously been the subject of other kleptoparasitic attempts. This justifies the assumption that each item of food can be treated as one unit of food regardless of the previous history of handling for that food item.

Appendix K – Algebraic solutions for conditions for using kleptoparasitism and defending/ resisting against kleptoparasitic attacks

K.1 – When to attack AGG (handler defends and population defends):

$$\frac{t_a}{2} + (1-\alpha)T_s < \frac{1}{v_f f} \quad (1)$$

$$\frac{t_a}{2} + (1-\alpha)\frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} < \frac{1}{v_f f} \quad (2)$$

$$t_a + 2(1-\alpha)\frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} < \frac{2}{v_f f} \quad (3)$$

$$t_a + (2-2\alpha)\frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} < \frac{2}{v_f f} \quad (4)$$

$$v_f f t_a + 2\frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} - 2\alpha\frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} < 2 \quad (5)$$

$$v_f f t_a - 2\alpha\frac{1 + \frac{v_h t_a H}{2}}{v_f f + \alpha v_h H} < 2 - 2\frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} \quad (6)$$

$$v_f f t_a - 2\alpha < 0 \quad (7)$$

$$v_f f t_a < 2\alpha \quad (8)$$

Condition A1a:

$$\boldsymbol{v_f f < \frac{2\alpha}{t_a}} \quad (9)$$

K.2 – When to attack ST (handler resists and population resists):

$$\frac{t_c}{2} + (1-\beta)T_s^* + \beta(1-x)T_s^* < \frac{1}{v_f f} \quad (10)$$

$$\frac{t_c}{2} + (1-\beta)\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} + \beta(1-x)\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} < \frac{1}{v_f f} \quad (11)$$

$$t_c + (2-2\beta)\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} + (2\beta - 2\beta x)\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} < \frac{2}{v_f f} \quad (12)$$

$$t_c + 2\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} - 2\beta\frac{1+\frac{v_h t_c H}{2}}{v_f f + \beta v_h H} + 2\beta\frac{1+\frac{v_h t_c H}{2}}{v_f f + \beta v_h H} - 2\beta x\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} < \frac{2}{v_f f} \quad (13)$$

$$t_c + 2\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} - 2\beta x\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} < \frac{2}{v_f f} \quad (14)$$

$$v_f f t_c + 2\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} v_f f - 2\beta x\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} v_f f < 2 \quad (15)$$

$$v_f f t_c - 2\beta x\frac{1+\frac{v_h t_c H}{2}}{v_f f + \beta v_h H} v_f f < 2 - 2\frac{1+v_h t_c H/2}{v_f f + \beta v_h H} v_f f \quad (16)$$

$$v_f f t_c - 2\beta x < 0 \quad (17)$$

$$v_f f t_c < 2\beta x \quad (18)$$

Condition A1b:

$$\boldsymbol{v_f f < \frac{2\beta x}{t_c}} \quad (19)$$

K.3 – When to defend against AGG (handler is an AGG kleptoparasite when it reverts to searching):

$$\frac{t_a}{2} + \alpha T_s < T_s \quad (20)$$

$$\frac{t_a}{2} + \alpha\frac{1+v_h t_a H/2}{v_f f + \alpha v_h H} < \frac{1+v_h t_a H/2}{v_f f + \alpha v_h H} \quad (21)$$

$$\frac{t_a}{2} + \frac{\alpha + \alpha v_h t_a H/2}{v_f f + \alpha v_h H} < \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} \quad (22)$$

$$\frac{v_f f t_a}{2} + \frac{\alpha v_h t_a H}{2} + \frac{\alpha v_h t_a H}{2} < 1 - \alpha + \frac{v_h t_a H}{2} \quad (23)$$

$$v_f f t_a + \alpha v_h t_a H + \alpha v_h t_a H < 2(1 - \alpha) + v_h t_a H \quad (24)$$

$$v_f f t_a + 2\alpha v_h t_a H < 2(1 - \alpha) + v_h t_a H \quad (25)$$

$$v_f f t_a < 2(1 - \alpha) + v_h t_a H - 2\alpha v_h t_a H \quad (26)$$

$$v_f f t_a < 2(1 - \alpha) + (1 - 2\alpha) v_h t_a H \quad (27)$$

Condition A3:

$$\boldsymbol{v_f f < \frac{2(1-\alpha)}{t_a} 2(1-\alpha) + (1-2\alpha) v_h H} \quad (28)$$

K.4 – When to defend against AGG (handler is an ST kleptoparasite when it reverts to searching:

$$\frac{t_a}{2} + \alpha T_s^* < T_s^* \quad (29)$$

$$\frac{t_a}{2} + \alpha \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H} < \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H} \quad (30)$$

$$\frac{t_a}{2} + \frac{\alpha + \alpha v_h t_c H/2}{v_f f + \beta v_h H} < \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H} \quad (31)$$

$$\frac{v_f f t_a}{2} + \frac{\beta v_h t_a H}{2} + \frac{\alpha v_h t_c H}{2} < 1 - \alpha + \frac{v_h t_c H}{2} \quad (32)$$

$$v_f f t_a + \beta v_h t_a H + \alpha v_h t_c H < 2(1 - \alpha) + v_h t_c H \quad (33)$$

$$v_f f t_a + \beta v_h t_a H < 2(1 - \alpha) + v_h t_c H - \alpha v_h t_c H \quad (34)$$

$$v_f f t_a + \beta v_h t_a H < 2(1-\alpha) + (1-\alpha) v_h t_c H \quad (35)$$

$$v_f f < \frac{2(1-\alpha) + (1-\alpha) v_h t_c H}{t_a} - \beta v_h H \quad (36)$$

Condition A4:

$$\boldsymbol{v_f f < \frac{(1-\alpha)(2 + v_h t_c H)}{t_a} - \beta v_h H} \quad (37)$$

K.5 – When to resist against ST (handler is an ST kleptoparasite when it reverts to searching:

$$\frac{t_c}{2} + \beta x T_s^* < T_s^* \quad (38)$$

$$\frac{t_c}{2} + \beta x \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H} < \frac{1 + v_h t_c H/2}{v_f f + \beta v_h H} \quad (39)$$

$$\frac{t_c}{2} + \frac{\beta x + \frac{\beta x v_h t_c H}{2}}{v_f f + \beta v_h H} < \frac{1 + \frac{v_h t_c H}{2}}{v_f f + \beta v_h H} \quad (40)$$

$$\frac{v_f f t_c}{2} + \frac{\beta v_h t_c H}{2} + \frac{\beta x v_h t_c H}{2} < 1 - \beta x + \frac{v_h t_c H}{2} \quad (41)$$

$$v_f f t_c + \beta v_h t_c H + \beta x v_h t_c H < 2(1 - \beta x) + v_h t_c H \quad (42)$$

$$v_f f t_c < 2(1 - \beta x) + v_h t_c H - \beta v_h t_c H - \beta x v_h t_c H \quad (43)$$

$$v_f f t_c < 2(1 - \beta x) + (1 - \beta - \beta x) v_h t_c H \quad (44)$$

Condition A5:

$$\boldsymbol{v_f f < \frac{2(1 - \beta x)}{t_c} + (1 - \beta - \beta x) v_h H} \quad (45)$$

K.6 – When to resist against ST (handler is an AGG kleptoparasite when it reverts to searching:

$$\frac{t_c}{2} + \beta x T_s < T_s \tag{46}$$

$$\frac{t_c}{2} + \beta x \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} < \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H} \tag{47}$$

$$\frac{v_f f t_c}{2} + \frac{\alpha v_h t_c H}{2} + \frac{\beta x v_h t_a H}{2} < 1 - \beta x + \frac{v_h t_a H}{2} \tag{48}$$

$$v_f f t_c + \alpha v_h t_c H + \beta x v_h t_a H < 2(1 - \beta x) + v_h t_a H \tag{49}$$

$$v_f f t_c < 2(1 - \beta x) + (1 - \beta x) v_h t_a H - \alpha v_h t_c H \tag{50}$$

$$v_f f < \frac{2(1 - \beta x) + (1 - \beta x) v_h t_a H}{t_c} - \alpha v_h H \tag{51}$$

Condition A6:

$$\boldsymbol{v_f f < \frac{(1 - \beta x)(2 + v_h t_a H)}{t_c} - \alpha v_h H} \tag{52}$$

K.7 – When to defend against AGG (population surrenders):

$$T_s^+ = \frac{1}{v_f f + v_h H} \tag{53}$$

$$\frac{t_a}{2} + \alpha T_s^+ < T_s^+ \tag{54}$$

$$\frac{t_a}{2} + \alpha \left(\frac{1}{v_f f + v_h H} \right) < \frac{1}{v_f f + v_h H} \tag{55}$$

$$\frac{t_a}{2} + \frac{\alpha}{v_f f + v_h H} < \frac{1}{v_f f + v_h H} \tag{56}$$

$$\frac{t_a v_f f}{2} + \frac{t_a v_h H}{2} < 1 - \alpha \quad (57)$$

$$t_a v_f f + t_a v_h H < 2(1 - \alpha) \quad (58)$$

$$t_a v_f f < 2(1 - \alpha) - v_h t_a H \quad (59)$$

Condition A7:

$$\boldsymbol{v_f f < \frac{2(1-\alpha)}{t_a} - v_h H} \quad (60)$$

K.8 – When to resist against ST (population surrenders):

$$\frac{t_c}{2} + \beta x T_s^+ < T_s^+ \quad (61)$$

$$\frac{t_c}{2} + \beta x \left(\frac{1}{v_f f + v_h H}\right) < \frac{1}{v_f f + v_h H} \quad (62)$$

$$\frac{t_c}{2} + \frac{\beta x}{v_f f + v_h H} < \frac{1}{v_f f + v_h H} \quad (63)$$

$$\frac{v_f f t_c}{2} + \frac{v_h t_c H}{2} < 1 - \beta x \quad (64)$$

$$v_f f t_c + v_h t_c H < 2(1 - \beta x) \quad (65)$$

$$v_f f t_c < 2(1 - \beta x) - v_h t_c H \quad (66)$$

Condition A8:

$$\boldsymbol{v_f f < \frac{2(1-\beta x)}{t_c} - v_h H} \quad (67)$$

K.9 – When to defend against AGG (population does not use kleptoparasitism and a mutant searcher attacks the handler):

$$T_s' = \frac{1}{v_f f} \tag{68}$$

$$\frac{t_a}{2} + \alpha T_s' < T_s' \tag{69}$$

$$\frac{t_a}{2} + \alpha\left(\frac{1}{v_f f}\right) < \frac{1}{v_f f} \tag{70}$$

$$\frac{t_a}{2} + \frac{\alpha}{v_f f} < \frac{1}{v_f f} \tag{71}$$

$$\frac{v_f f t_a}{2} < 1 - \alpha \tag{72}$$

$$v_f f t_a < 2(1 - \alpha) \tag{73}$$

Condition A9:

$$\boldsymbol{v_f f < \frac{2(1-\alpha)}{t_a}} \tag{74}$$

K.10 – When to resist against ST (population does not use kleptoparasitism and a mutant searcher attacks the handler):

$$\frac{t_c}{2} + \beta x T_s' < T_s' \tag{75}$$

$$\frac{t_c}{2} + \beta x\left(\frac{1}{v_f f}\right) < \frac{1}{v_f f} \tag{76}$$

$$\frac{t_c}{2} + \frac{\beta x}{v_f f} < \frac{1}{v_f f} \tag{77}$$

$$\frac{v_f t_c}{2} < 1 - \beta x \tag{78}$$

$$v_f t_c < 2(1 - \beta x) \tag{79}$$

Condition A10:

$$\boldsymbol{v_f f < \frac{2(1 - \beta x)}{t_c}} \tag{80}$$

Appendix L – Summary tables of all information-theoretic models analysed for Study 1

Table L1. One predictor main effects models (Models 1 to 5).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
1				452.69	677	738.64	1657.6
Constant	0.22 [0.15, 0.29]	0.03	<0.001				
Site	-1.73 [-1.92, -1.55]	0.09	<0.001				
2				582.87	675	738.64	1833.3
Constant	-0.60 [-0.86, -0.35]	0.13	<0.001				
SpeciesCG	-1.07 [-1.52, -0.62]	0.23	<0.001				
SpeciesGBB	0.79 [0.50, 1.08]	0.15	<0.001				
SpeciesHG	0.68 [0.41, 0.95]	0.14	<0.001				
3				675.46	677	738.64	1929.4
Constant	0.08 [-0.04, 0.20]	0.06	0.21				
Season	-0.13 [-0.28, 0.03]	0.08	0.11				
4				573.47	677	738.64	1818.2
Constant	<0.01 [-0.07, 0.07]	0.03	1				
Std Prey	0.04 [0.32, 0.46]	0.03	<0.001				
5				388.58	677	738.64	1554
Constant	<0.01 [-0.06, 0.06]	0.03	1				
Std Pop'n	0.65 [0.60, 0.71]	0.03	<0.001				

Table L2. Main effects models containing only two predictor variables (Models 6 to 15).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
6				451.40	674	735.51	1661.8
Constant	0.14 [-0.11, 0.39]	0.13	0.27				
Site	-1.64 [-1.87, -1.41]	0.12	<0.001				
SpeciesCG	-0.17 [-0.59, 0.25]	0.21	0.43				
Species GBB	0.10 [-0.17, 0.37]	0.14	0.46				
SpeciesHG	0.07 [-0.18, 0.33]	0.14	0.57				
7				452.55	676	737.60	1659.4
Constant	0.20 [0.10, 0.30]	0.05	<0.001				
Site	-1.74 [-1.92, -1.55]	0.10	<0.001				
Season	0.03 [-0.10, 0.16]	0.07	0.65				
8				433.57	676	737.60	1630.3
Constant	0.19 [0.12, 0.26]	0.03	<0.001				
Site	-1.50 [-1.70, -1.30]	0.10	<0.001				
Std Prey	0.18 [0.12, 0.25]	0.03	<0.001				
9				344.18	676	737.60	1573.6
Constant	0.12 [0.06, 0.18]	0.03	<0.001				
Site	-0.93 [-1.12, -0.73]	0.10	<0.001				
Std Pop'n	0.48 [0.42, 0.55]	0.03	<0.001				
10				344.18	676	737.60	1473.6
Constant	-0,62 [-0.90, -0.33]	0.14	<0.001				
SpeciesCG	-1.07 [-1.52, -0.62]	0.23	<0.001				
SpeciesGBB	0.80 [0.51, 1.09]	0.15	<0.001				
SpeciesHG	0.69 [0.41, 0.96]	0.14	<0.001				
Season	0.02 [-0.13, 0.17]	0.08	0.80				
11				523.13	674	735.51	1761.8
Constant	-0.41 [-0.66, -0.17]	0.13	<0.001				
SpeciesCG	-0.90 [-1.33, -0.47]	0.22	<0.001				
SpeciesGBB	0.52 [0.24, 0.80]	0.14	<0.001				

SpeciesHG	0.49 [0.24, 0.75]	0.13	<0.001				
Std Prey	0.31 [0.24, 0.38]	0.04	<0.001				
12				370.55	674	735.51	1527.7
Constant	-0.23 [-0.43, -0.02]	0.11	0.03				
SpeciesCG	-0.57 [-0.94, -0.21]	0.19	<0.01				
SpeciesGBB	0.33 [0.09, 0.56]	0.12	<0.01				
SpeciesHG	0.25 [0.03, 0.47]	0.11	0.02				
Std Pop'n	0.60 [0.54, 0.65]	0.03	<0.001				
13				559.23	676	737.60	1803.1
Constant	0.19 [0.08, 0.30]	0.06	<0.001				
Season	-0.31 [-0.45, -0.16]	0.07	<0.001				
Std Prey	0.42 [0.35, 0.49]	0.04	<0.001				
14				388.07	676	737.60	1555.1
Constant	-0.04 [-0.13, 0.06]	0.05	0.45				
Season	0.06 [-0.06, 0.18]	0.06	0.34				
Std Pop'n	0.66 [0.60, 0.71]	0.03	<0.001				
15				376.89	676	737.60	1535.2
Constant	<0.001 [-0.06, 0.06]	0.02	1				
Std Prey	0.14 [0.08, 0.21]	0.03	<0.001				
Std Pop'n	0.59 [0.53, 0.65]	0.03	<0.001				

Table L3. Main effects models containing 3 predictor variables (Models 16 to 21).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
16				451.2	673	734.46	1663.4
Constant	0.11 [-0.16, 0.37]	0.14	0.44				
Site	-1.64 [-1.87, -1.41]	0.12	<0.001				
SpeciesCG	-0.17 [-0.59, 0.24]	0.21	0.42				
SpeciesGBB	0.11 [-0.16, 0.39]	0.14	0.41				
SpeciesHG	0.08 [-0.17, 0.34]	0.13	0.53				
Season	0.04 [-0.09, 0.17]	0.07	0.52				
17				432.78	673	734.46	1635.1
Constant	0.16 [-0.09, 0.40]	0.12	0.21				
Site	-1.43 [-1.67, -1.20]	0.12	<0.001				
SpeciesCG	-0.18 [-0.59, 0.23]	0.21	0.39				
SpeciesGBB	0.03 [-0.24, 0.29]	0.14	0.84				
SpeciesHG	0.04 [-0.21, 0.29]	0.13	0.75				
Std Prey	0.18 [0.12, 0.25]	0.03	<0.001				
18				343.10	673	734.46	1477.4
Constant	0.09 [-0.13, 0.30]	0.11	0.44				
Site	-0.85 [-1.08, -0.62]	0.12	<0.001				
SpeciesCG	-0.20 [-0.57, 0.16]	0.19	0.27				
SpeciesGBB	0.06 [-0.18, 0.30]	0.12	0.62				
SpeciesHG	0.02 [-0.20, 0.24]	0.11	0.86				
Std Pop'n	0.48 [0.42, 0.55]	0.03	<0.001				
19				432.71	675	736.55	1631
Constant	0.23 [0.13, 0.33]	0.05	<0.001				
Site	-1.47 [-1.68, -1.27]	0.10	<0.001				
Season	-0.08 [-0.21, 0.05]	0.07	0.25				
Prey	0.20 [0.13, 0.27]	0.04	<0.001				
20				432.81	675	736.55	1472.9
Constant	0.06 [-0.03, 0.15]	0.05	0.19				

Site	-0.94 [-1.13, -0.74]	0.10	<0.001				
Season	0.09 [-0.02, 0.21]	0.06	0.10				
Std Pop'n	0.49 [0.42, 0.55]	0.03	<0.001				
21				340.73	675	736.55	1468.7
Constant	0.11 [0.05, 0.16]	0.03	<0.001				
Site	-0.86 [-1.06, -0.66]	0.10	<0.001				
Std Prey	0.08 [0.02, 0.14]	0.03	<0.01				
Std Pop'n	0.46 [0.39, 0.53]	0.03	<0.001				

Table L4. Interaction and main effects models containing 2 predictor variables (Models 22 to 31).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
22				436.92	672	733.42	1643.6
Constant	-0.25 [-0.55, 0.04]	0.15	0.09				
Site	-0.76 [-1.21, -0.32]	0.23	<0.001				
SpeciesCG	-0.65 [-1.11, -0.19]	0.24	<0.001				
SpeciesGBB	0.52 [0.20, 0.84]	0.16	<0.001				
SpeciesHG	0.49 [0.18, 0.80]	0.16	<0.001				
Site:CG	NA	NA	NA				
Site:GBB	-1.64 [-2.44, -0.85]	0.40	<0.001				
Site:HG	-1.09 [-1.62, -0.57]	0.27	<0.001				
23				447.81	675	736.55	1654.3
Constant	0.23 [0.13, 0.33]	0.05	<0.001				
Site	-2.21 [-2.60, -1.82]	0.20	<0.001				
Season	-0.03 [-0.16, 0.11]	0.07	0.71				
Site: Season	0.61 [0.16, 1.05]	0.23	<0.001				
24				429.61	675	736.55	1626.1
Constant	0.19 [0.12, 0.25]	0.03	<0.001				
Site	-2.41 [-3.15, -1.67]	0.38	<0.001				
Std Prey	0.19 [0.13, 0.26]	0.03	<0.001				
Site: Prey	-0.84 [-1.50, -0.18]	0.34	0.01				
25				344.17	675	736.55	1475.5
Constant	0.12 [0.06, 0.18]	0.03	<0.001				
Site	-1.87 [-15.49, 11.74]	6.95	0.79				
Std Pop'n	0.48 [0.42, 0.55]	0.03	<0.001				
Site: Pop'n	-0.65 [-9.96, 8.67]	-0.65	0.89				
26				579.65	671	732.37	1837.5
Constant	-1.13 [-1.74, -0.53]	0.31	<0.001				
SpeciesCG	-0.73 [-2.65, 1.19]	0.98	0.45				
SpeciesGBB	1.35 [0.71, 1.98]	0.32	<0.001				

SpeciesHG	1.22 [0.59, 1.84]	0.32	<0.001				
Season	0.65 [-0.02, 1.32]	0.34	0.06				
CG:Season	-0.44 [-2.42, 1.54]	1	0.66				
GBB: Season	-0.69 [-1.41, 0.03]	0.37	0.06				
HG:Season	-0.65 [-1.34, 0.05]	0.35	0.07				
27				518.51	671	732.37	1761.8
Constant	-0.33 [-0.63, -0.03]	0.15	0.03				
SpeciesCG	-1.51 [-3.57, 0.55]	1.05	0.15				
SpeciesGBB	0.47 [0.14, 0.79]	0.17	<0.01				
SpeciesHG	0.41 [0.10, 0.72]	0.16	0.01				
Std Prey	0.46 [0.16, 0.76]	0.15	<0.01				
CG:Prey	-0.60 [-2.38, 1.17]	0.91	0.51				
GBB:Prey	-0.28 [-0.61, 0.04]	0.17	0.09				
HG:Prey	-0.11 [-0.42, 0.20]	0.16	0.50				
28				360.69	671	732.37	1515.4
Constant	-0.38 [-0.61, -0.14]	0.12	<0.01				
SpeciesCG	-7.71 [-30.25, 14.83]	11.50	0.50				
SpeciesGBB	0.50 [0.25, 0.76]	0.13	<0.001				
SpeciesHG	0.40 [0.15, 0.64]	0.12	<0.01				
Std Pop'n	0.35 [0.17, 0.54]	0.10	<0.001				
CG:Pop'n	-4.75 [-20.20, 10.70]	7.88	0.55				
GBB:Pop'n	0.10 [-0.12, 0.32]	0.11	0.35				
HG:Pop'n	0.33 [0.13, 0.54]	0.10	<0.01				
29				556.83	675	736.55	1802.2
Constant	0.22 [0.10, 0.33]	0.06	<0.001				
Season	-0.33 [-0.47, -0.18]	0.07	<0.001				
Std Prey	0.52 [0.39, 0.66]	0.07	<0.001				
Season:Prey	-0.14 [-0.29, 0.02]	0.08	0.09				
30				678.00	678	736.55	1556.6
Constant	-0.03	0.05	0.51				

	[-0.13, 0.06]						
Season	0.06 [-0.06, 0.17]	0.06	0.36				
Std Pop'n	0.63 [0.54, 0.72]	0.05	<0.001				
Season:Pop'n	0.04 [-0.08, 0.16]	0.06	0.52				
31				369.17	675	736.55	1523.2
Constant	0.04 [-0.02, 0.10]	0.03	0.16				
Std Prey	0.14 [0.08, 0.20]	0.03	<0.001				
Std Pop'n	0.61 [0.54, 0.67]	0.03	<0.001				
Prey:Pop'n	-0.10 [-0.16, -0.05]	0.03	<0.001				

Table L5. Interaction and main effects models containing 3 predictor variables (Models 32 to 37).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
32				428.44	665	726.10	1644.3
Constant	-0.64 [-1.28, -0.01]	0.32	0.05				
Site	-1.47 [-2.58, -0.36]	0.57	0.01				
SpeciesCG	0.25 [-1.57, 2.06]	0.93	0.79				
SpeciesGBB	0.88 [0.21, 1.54]	0.34	0.01				
SpeciesHG	0.91 [0.26, 1.57]	0.33	0.01				
Season	0.49 [-0.23, 1.22]	0.37	0.18				
Site:CG	NA	NA	NA				
Site:GBB	-0.51 [-2.44, 1.43]	0.99	0.61				
Site:HG	-0.77 [-1.97, 0.44]	0.61	0.21				
Site:Season	0.76 [-0.45, 1.98]	0.62	0.22				
CG:Season	-1.05 [-2.93, 0.83]	0.96	0.27				
GBB:Season	-0.43 [-1.19, 0.33]	0.39	0.27				
HG:Season	-0.56 [-1.30, 0.19]	0.38	0.14				
Site:CG:Seas	NA	NA	NA				
Site:GBB:Seas	-1.30 [-3.43, 0.82]	1.08	0.23				
Site:HG:Seas	-0.14 [-1.49, 1.20]	0.69	0.84				
33				414.8	665	726.10	1622.3
Constant	-0.24 [-0.53, 0.05]	0.15	0.11				
Site	1.34 [-4.33, 7.01]	2.89	0.64				
SpeciesCG	-2.93 [-8.88, 3.02]	3.04	0.34				
SpeciesGBB	0.48 [0.16, 0.80]	0.16	<0.01				
SpeciesHG	0.45 [0.15, 0.75]	0.16	<0.01				
Std Prey	0.25 [-0.14, 0.63]	0.19	0.21				
Site:CG	NA	NA	NA				
Site:GBB	-3.98 [-9.91, 1.94]	3.02	0.19				
Site:HG	-3.36 [-9.12, 2.40]	2.94	0.25				
Site:Prey	1.46 [-3.12, 6.03]	2.33	0.53				
CG:Prey	-1.85 [-6.67, 2.97]	2.46	0.45				

GBB:Prey	-0.16 [-0.57, 0.25]	0.21	0.44				
HG:Prey	-0.02 [-0.41, 0.37]	0.20	0.92				
Site:CG:Prey	NA	NA	NA				
Site:GBB:Prey	-1.90 [-6.94, 3.14]	2.57	0.46				
Site:HG:Prey	-1.87 [-6.55, 2.80]	2.39	0.43				
34				318.86	665	726.10	1443.7
Constant	-0.27 [-0.52, -0.01]	0.13	0.04				
Site	-12.62 [-67.14, 41.94]	27.84	0.65				
SpeciesCG	4.80 [-53.76, 63.36]	29.88	0.87				
SpeciesGBB	0.47 [0.19, 0.74]	0.14	<0.01				
SpeciesHG	0.37 [0.10, 0.64]	0.14	<0.01				
Std Pop'n	0.21 [-0.04, 0.46]	0.13	0.11				
Site:CG	NA	NA	NA				
Site:GBB	19.35 [-40.08, 78.77]	30.32	0.52				
Site:HG	57.92 [-6.11, 121.95]	32.67	0.08				
Site:Pop'n	-8.30 [-45.52, 28.92]	18.99	0.66				
CG:Pop'n	3.70 [-36.28, 43.67]	20.40	0.86				
GBB:Pop'n	0.14 [-0.14, 0.41]	0.14	0.33				
HG:Pop'n	0.36 [0.10, 0.62]	0.13	<0.01				
Site:CG:Pop'n	NA	NA	NA				
Site:GBB:Pop'n	14.23 [-26.39, 54.85]	20.73	0.49				
Site:HG:Pop'n	39.88 [-3.93, 83.58]	22.30	0.07				
35				415.58	671	732.37	1609.9
Constant	0.32 [0.21, 0.42]	0.05	<0.001				
Site	-2.11 [-3.20, -1.03]	0.55	<0.001				
Season	-0.16 [-0.30, -0.03]	0.07	0.02				
Std Prey	0.39 [0.27, 0.51]	0.06	<0.001				
Site:Season	-0.43 [-1.90, 1.04]	0.75	0.57				
Site:Prey	-0.21 [-1.26, 0.84]	0.53	0.67				
Season:Prey	-0.25 [-0.40, -0.10]	0.08	<0.01				
Site:Seas:Prey	-0.82 [-2.18, 0.54]	0.69	0.24				

36				338.29	671	732.37	1471.8
Constant	0.09 [-0.006, 0.18]	0.05	0.07				
Site	-36.70 [-641.17, 119.48]	79.68	0.65				
Season	0.05 [-0.007, 0.17]	0.06	0.44				
Std Pop'n	0.49 [0.39, 0.58]	0.05	<0.001				
Site:Season	26.50 [-130.34, 183.35]	80.03	0.74				
Site:Pop'n	-24.01 [-130.05, 82.04]	54.11	0.66				
Season:Pop'n	-0.01 [-0.14, 0.12]	0.07	0.90				
Site:Seas:Pop'n	17.59 [-88.93, 124. 10]	54.34	0.75				
37				337.01	671	732.37	1469.3
Constant	0.10 [0.04, 0.16]	0.03	<0.001				
Site	0.16 [-70.10, 70.42]	35.85	0.99				
Std Prey	0.08 [0.02, 0.14]	0.03	<0.01				
Std Pop'n	0.44 [0.37, 0.51]	0.04	<0.001				
Site:Prey	0.87 [-69.40, 71.14]	35.85	0.98				
Site:Pop'n	1.26 [-46.70, 49.22]	24.47	0.96				
Prey:Pop'n	0.04 [-0.03, 0.10]	0.03	0.25				
Site:Prey:Pop'n	1.06 [-46.90, 49.01]	24.47	0.97				

Table L6. Main effects models containing 4 predictor variables (Models 38 to 42).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
38				432.08	672	733.42	1635.9
Constant	0.22 [-0.05, 0.48]	0.14	0.11				
Site	-1.42 [-1.66, -1.18]	0.12	<0.001				
SpeciesCG	-0.17 [-0.58, 0.24]	0.21	0.41				
SpeciesGBB	0.01 [-0.27, 0.27]	0.14	0.99				
SpeciesHG	0.02 [-0.23, 0.27]	0.13	0.85				
Season	-0.07 [-0.21, 0.06]	0.07	0.28				
Std Prey	0.20 [0.13, 0.27]	0.04	<0.001				
39				431.37	678	733.42	1476
Constant	-0.01 [-0.24, 0.23]	0.12	0.99				
Site	-0.85 [-1.07, -0.62]	0.12	<0.001				
SpeciesCG	-0.22 [-0.58, 0.15]	0.19	0.25				
SpeciesGBB	0.09 [-0.15, 0.33]	0.12	0.46				
SpeciesHG	0.04 [-0.18, 0.26]	0.11	0.73				
Season	0.11 [-0.01, 0.22]	0.06	0.07				
Std Pop'n	0.49 [0.42, 0.55]	0.03	<0.001				
40				339.88	672	733.42	1473
Constant	0.09 [-0.12, 0.31]	0.11	0.38				
Site	-0.80 [-1.03, -0.57]	0.12	<0.001				
SpeciesCG	-0.21 [-0.57, 0.16]	0.18	0.26				
SpeciesGBB	0.03 [-0.21, 0.27]	0.12	0.81				
SpeciesHG	0.01 [-0.21, 0.23]	0.11	0.94				
Std Prey	0.08 [0.02, 0.14]	0.03	0.01				
Std Pop'n	0.46 [0.39, 0.53]	0.03	<0.001				
41				340.36	674	733.42	1470
Constant	0.08 [-0.01, 0.17]	0.05	0.09				
Site	-0.87 [-1.08, -0.67]	0.10	<0.001				
Season	0.05 [-0.07, 0.17]	0.06	0.39				

Std Prey	0.07 [0.01, 0.14]	0.03	0.03				
Std Pop'n	0.46 [0.38, 0.53]	0.03	<0.001				
42				362.96	672	732.42	1517.6
Constant	-0.22 [-0.45, 0.01]	0.12	0.06				
SpeciesCG	-0.55 [-0.91, -0.19]	0.18	<0.01				
SpeciesGBB	0.27 [0.03, 0.51]	0.12	0.03				
SpeciesHG	0.22 [0.01, 0.44]	0.11	0.05				
Season	0.04 [-0.08, 0.17]	0.06	0.51				
Std Prey	0.11 [0.04, 0.18]	0.03	<0.01				
StdPop'n	0.56 [0.49, 0.62]	0.03	<0.001				

Table L7. Interaction and main effects models containing 4 predictor variables (Models 43 to 47).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
43				39.15	653	713.56	1604.7
Constant	-1.28 [-3.64, 1.08]	1.20	0.29				
Site	-6.63 [-54.90, 41.64]	24.63	0.79				
SpeciesCG	1.80 [-16.06, 19.66]	9.11	0.84				
SpeciesGBB	1.53 [-0.85, 3.88]	1.21	0.21				
SpeciesHG	1.74 [-0.63, 4.10]	1.20	0.15				
Season	1.10 [-1.28, 3.48]	1.21	0.36				
Std Prey	-0.73 [-3.33, 1.87]	1.32	0.58				
Site:CG	NA	NA	NA				
Site:GBB	3.22 [-36.47, 42.90]	20.25	0.87				
Site:HG	4.27 [-44.02, 52.56]	24.64	0.86				
Site:Season	6.65 [-41.95, 55.26]	24.80	0.79				
Site:Prey	-3.80 [-41.62, 34.00]	19.29	0.84				
CG:Season	-3.40 [-20.93, 14.13]	8.94	0.70				
GBB:Season	-1.07 [-3.47, 1.32]	1.22	0.38				
HG:Season	-1.40 [-3.79, 0.98]	1.22	0.25				
CG:Prey	-0.65 [-5.53, 4.73]	2.49	0.79				
GBB:Prey	0.86 [-1.75, 3.46]	1.33	0.52				
HG:Prey	1.30 [-1.30, 3.90]	1.33	0.33				
Season:Prey	0.90 [-1.74, 3.54]	1.35	0.50				
Site:CG:Season	NA	NA	NA				
Site:GBB:Season	-7.57 [-47.56, 32.43]	20.41	0.71				
Site:HG:Season	-6.10 [-54.75, 42.55]	24.82	0.81				
Site:CG:Prey	NA	NA	NA				
Site:GBB:Prey	-2.60 [-8.30, 3.11]	2.91	0.37				
Site:HG:Prey	3.29 [-34.54, 41.12]	19.30	0.86				
Site:Season:Prey	4.21 [-33.89, 42.30]	19.43	0.83				
CG:Season:Prey	NA	NA	NA				
GBB:Season:Prey	-0.97 [-3.62, 1.68]	1.35	0.47				
HG:Season:Prey	-1.32	1.35	0.33				

	[-3.97. 1.32]						
Site:CG:Seas:Prey	NA	NA	NA				
Site:GBB:Seas:Prey	NA	NA	NA				
Site:HG:Seas:Prey	-4.08 [-42.22, 34.06]	19.46	0.83				
44				308.97	653	713.56	1446.3
Constant	-7.64 [-17.53, 2.25]	5.05	0.13				
Site	-302.79 [-956.04, 350.45]	333.29	0.36				
SpeciesCG	46.57 [-17.14, 110.27]	32.50	0.15				
SpeciesGBB	7.80 [-2.09, 17.70]	5.05	0.12				
SpeciesHG	7.69 [-2.20, 17.58]	5.05	0.13				
Season	7.45 [-2.45, 17.35]	5.05	0.14				
Std Pop'n	-13.63 [-32.88, 5.62]	9.82	0.17				
Site:CG	NA	NA	NA				
Site:GBB	79.66 [11.65, 147.66]	34.70	0.02				
Site:HG	278.06 [-395.33, 951.46]	343.57	0.42				
Site:Season	249.60 [-406.37, 905.56]	334.68	0.46				
Site:Pop'n	-195.54 [-639.09, 248.01]	226.30	0.39				
CG:Season	-1.81 [-3.87, 0.25]	1.05	0.09				
GBB:Season	-7.39 [-17.29, 2.51]	5.05	0.14				
HG:Season	-7.38 [-17.28, 2.52]	5.05	0.14				
CG:Pop'n	31.09 [-12.20, 74.37]	22.08	0.16				
GBB:Pop'n	13.92 [-5.34, 33.17]	9.82	0.16				
HG:Pop'n	14.23 [-5.02, 33.48]	9.82	0.15				
Season:Pop;n	13.80 [-5.46, 33.05]	9.82	0.16				
Site:CG:Season	NA	NA	NA				
Site:GBB:Season	-14.94 [-33.58, 3.70]	9.51	0.12				
Site:HG:Season	-181.31 [-859.12, 496.50]	345.83	0.60				
Site:CG:Pop'n	NA	NA	NA				
Site:GBB:Pop'n	45.29 [0.96, 89.63]	22.62	0.05				
Site:HG:Pop'n	179.52	233.29	0.44				

	[-277.72, 636.76]						
Site:Season:Pop'n	159.51 [-285.90, 604.93]	227.26	0.48				
CG:Season:Pop'n	NA	NA	NA				
GBB:Season:Pop'n	-13.65 [-32.91, 5.60]	9.82	0.17				
HG:Season:Pop'n	-13.84 [-33.09, 5.41]	9.82	0.16				
Site:CG:Seas:Pop	NA	NA	NA				
Site:GBB:Seas:Pop	NA	NA	NA				
Site:HG:Seas:Pop	-113.10 [-573.39, 347.18]	234.84	0.63				
45				678.00	651	711.47	1450.4
Constant	-0.28 [-0.55, -0.01]	0.14	0.04				
Site	-143.90 [-3368.04, 489.21]	984	0.14				
SpeciesCG	1563.00 [-371.39, 3497.87]	987.10	0.11				
SpeciesGBB	0.47 [0.18, 0.76]	0.15	<0.01				
SpeciesHG	0.37 [0.09, 0.65]	0.14	<0.01				
Std Prey	0.22 [-0.15, 0.59]	0.19	0.25				
Std Pop'n	0.13 [-0.15, 0.41]	0.14	0.35				
Site:CG	NA	NA	NA				
Site:GBB	1382 [-556.31, 3319.46]	988.70	0.16				
Site:HG	1394 [-538.60, 3327.39]	986.20	0.16				
Site:Prey	-1060.00 [-2573.25, 453.37]	772.20	0.17				
Site:Pop'n	-999.30 [-2332.06, 353.37]	680	0.14				
CG:Prey	1214.00 [-309.35, 2737.80]	777.30	0.12				
GBB:Prey	-0.19 [-0.58, 0.19]	0.19	0.33				
HG:Prey	-0.14 [-0.52, 0.24]	0.19	0.47				
CG:Pop'n	1085 [-251.96, 2421.56]	682	0.11				
GBB:Pop'n	0.17 [-0.15, 0.48]	0.16	0.30				
HG:Pop'n	0.39	0.15	0.01				

	[0.09, 0.68]						
Prey:Pop'n	0.13 [-0.29, 0.56]	0.22	0.54				
Site:CG:Prey	NA	NA	NA				
Site:GBB:Prey	1001.00 [-521.02, 2523.98]	776.80	0.20				
Site:HG:Prey	969.20 [-549.34, 2487.72]	774.80	0.21				
Site:CG:Pop'n	NA	NA	NA				
Site:GBB:Pop'n	961.30 [-377.59, 2300.23]	683.10	0.16				
Site:HG:Pop'n	969.40 [-366.23, 2306.06]	681.50	0.16				
Site:Prey:Pop'n	-737.20 [-1782.89, 308.45]	533.50	0.17				
CG:Prey:Pop'n	842.70 [-209.89, 1895.33]	537.10	0.12				
GBB:Prey:Pop'n	-0.07 [-0.52, 0.37]	0.23	0.74				
HG:Prey:Pop'n	-0.09 [-0.53, 0.34]	0.22	0.68				
Site:CG:Prey:Pop	NA	NA	NA				
Site:GBB:Prey:Pop	697.40 [-354.41, 1749.41]	536.60	0.19				
Site:HG:Prey:Pop	675.40 [-373.82, 1724.56]	535.30	0.21				
46				319.99	663	724.01	1450.1
Constant	0.11 [0.01, 0.21]	0.05	0.03				
Site	18.04 [-492.80, 528.88]	260.64	0.94				
Season	0.03 [-0.09, 0.16]	0.07	0.63				
Std Prey	0.15 [0.02, 0.27]	0.06	0.02				
Std Pop'n	0.41 [0.31, 0.51]	0.05	<0.001				
Site:Season	21.31 [-496.64, 539.27]	264.27	0.94				
Site:Prey	56.70 [-482.17, 595.57]	274.94	0.84				
Site:Pop'n	13.13 [-333.51, 359.76]	176.86	0.94				
Season:Prey	-0.12 [-0.27, 0.02]	0.07	0.10				
Season:Pop'n	0.15	0.08	0.06				

	[-0.01, 0.30]						
Prey:Pop'n	0.18 [0.07, 0.28]	0.05	<0.001				
Site:Season:Prey	-10.89 [-556.29, 534.51]	278.27	0.97				
Site:Season:Pop'n	14.99 [-336.58, 366.56]	179.38	0.93				
Site:Prey:Pop'n	38.30 [-327.41, 404.01]	186.59	0.84				
Seas:Prey:Pop'n	-0.28 [-0.41, -0.14]	0.07	<0.001				
Site:Seas:Prey:Pop	-6.22 [-376.45, 364.01]	188.90	0.97				
47				320.35	650	710.42	1476.9
Constant	-2.09 [-23.79, 19.60]	11.07	0.85				
SpeciesCG	123.64 [-31.83, 279.11]	79.32	0.12				
SpeciesGBB	2.24 [-19.46, 3.93]	11.07	0.84				
SpeciesHG	2.04 [-19.65, 23.74]	11.07	0.85				
Season	1.83 [-19.86, 23.53]	11.07	0.87				
Std Prey	-2.09 [-19.04, 14.87]	8.65	0.81				
Std Pop'n	-1.59 [-44.88, 41.70]	22.09	0.94				
CG:Season	-0.22 [-15.45, 15.02]	7.77	0.98				
GBB:Season	-1.77 [-23.46, 19.93]	11.07	0.87				
HG:Season	-1.64 [23.34, 19.93]	11.07	0.88				
CG:Prey	154.97 [-24.99, 334.93	91.82	0.09				
GBB:Prey	2.17 [-14.78, 19.13]	8.65	0.80				
HG:Prey	2.27 [-14.69, 19.22]	8.65	0.79				
CG:Pop'n	85.02 [-20.72, 190.76]	539.5	0.12				
GBB:Pop'n	1.88 [-41.41, 45.17]	22.09	0.93				
HG:Pop'n	2.26 [-41.03, 45.55]	22.09	0.92				
Season:Prey	2.31 [14.65, 19.27]	8.65	0.79				
Season:Pop'n	1.78 [-41.51, 45.07]	22.09	0.94				
Prey:Pop'n	-2.66 [-36.43, 31.12]	17.23	0.80				

CG:Seas:Prey	NA	NA	NA
GBB:Seas:Prey	-2.41 [-19.37, 14.56]	8.65	0.78
HG:Seas:Prey	-2.47 [-19.43, 14.49]	8.65	0.78
CG:Seas:Pop'n	NA	NA	NA
GBB:Seas:Pop'n	-1.16 [-44.45, 42.13]	22.09	0.96
HG:Seas:Pop'n	-1.70 [-45.00, 41.59]	22.09	0.94
CG:Prey:Pop'n	106.02 [-16.96, 229.01]	62.75	0.09
GBB:Prey:Pop'n	2.70 [-31.07, 36.47]	17.23	0.88
HG:Prey:Pop'n	2.81 [-30.97, 36.58]	17.23	0.88
Seas:Prey:Pop'n	2.65 [-31.12, 36.43]	17.23	0.88
CG:Seas:Prey:Pop	NA	NA	NA
GBB:Seas:Prey:Pop	-3.02 [-36.80, 30.75]	17.23	0.86
HG:Seas:Prey:Pop	-3.02 [-36.80, 30.76]	17.23	0.86

Table L8. Interaction and main effects models containing all 5 predictor variables (Models 48 & 49).

Model	Coefficient [95% CI]	SE	P	Deviance	Df	Critical Value X^2	AIC
48				339.32	671	732.37	1473.9
Constant	0.04 [-0.19, 0.28]	0.12	0.73				
Site	-0.80 [-1.03, -0.57]	0.12	<0.001				
SpeciesCG	-0.21 [-0.58, 0.15]	0.18	0.25				
SpeciesGBB	0.05 [-0.19, 0.29]	0.12	0.67				
SpeciesHG	0.02 [-0.19, 0.24]	0.11	0.85				
Season	0.06 [-0.06, 0.18]	0.06	0.29				
Std Prey	0.07 [0.01, 0.13]	0.03	0.04				
Std Pop'n	0.47 [0.40, 0.53]	0.03	<0.001				
49				274.88	631	690.55	1410.9
Constant	-7.25 [-17.09, 2.58]	5.02	0.15				
Site	-2079 [-8555.08, 4396.29]	3304	0.53				
SpeciesCG	2371 [-3990.69, 8732.83]	3246	0.47				
SpeciesGBB	7.42 [-2.41, 17.26]	5.02	0.14				
SpeciesHG	7.26 [-2.58, 17.10]	5.02	0.15				
Season	7.03 [-2.81, 16.87]	5.02	0.16				
Std Prey	0.35 [-2.14, 2.83]	1.27	0.79				
Std Pop'n	-12.87 [-33.51, 7.78]	10.50	0.22				
Site:CG	NA	NA	NA				
Site:GBB	3053 [-3390.74, 9497.23]	3288	0.35				
Site:HG	2079 [-4359.27, 8516.43]	3285	0.53				
Site:Season	-145.10 [-1184.27, 894.16]	530.20	0.78				

Site:Prey	-1394 [-6501.80, 3714.35]	2606	0.59
Site:Pop'n	-1396 [-5789.58, 2998.20]	2242	0.53
CG:Season	-23.24 [-67.17, 20.69]	22.41	0.30
GBB:Season	-6.93 [-16.78, 2.91]	5.02	0.17
HG:Season	-6.88 [-16.73, 2.96]	5.02	0.17
CG:Prey	1761 [-3216.99, 6738.36]	2540	0.49
GBB:Prey	-0.27 [-2.77, 2.22]	1.27	0.83
HG:Prey	-0.27 [-2.77, 2.22]	1.27	0.83
CG:Pop'n	1630 [-2738.56, 5998.60]	2229	0.46
GBB:Pop'n	13.12 [-7.52, 33.77]	10.53	0.21
HG:Pop'n	13.37 [-7.27, 34.02]	10.53	0.20
Season:Prey	-0.19 [-2.70, 2.33]	1.28	0.88
Season:Pop'n	12.98 [-7.67, 33.63]	10.54	0.22
Prey:Pop'n	-0.69 [0.23, 1.14]	0.23	<0.01
Site:CG:Seas	NA	NA	NA
Site:GBB:Seas	-75.32 [-179.74, 29.10]	53.28	0.16
Site:HG:Seas	-51.25 [-762.87, 660.37]	363.10	0.89
Site:CG:Prey	NA	NA	NA
Site:GBB:Prey	2291 [-2714.06, 7296.24]	2554	0.37
Site:HG:Prey	1420 [-3653.19, 6493.08]	2588	0.58
Site:CG:Pop'n	NA	NA	NA
Site:GBB:Pop'n	2066 [-2320.75, 6453.48]	2238	0.37
Site:HG:Pop'n	1396 [-2972.26, 5764.14]	2229	0.53

Site:Season:Prey	-211.90 [-861.54, 437.69]	331.40	0.52
Site:Season:Pop	-149.20 [-850.96, 552.50]	358	0.68
Site:Prey:Pop'n	-941.60 [-4407.78, 2524.63]	1769	0.59
CG:Seas:Prey	NA	NA	NA
GBB:Seas:Prey	-0.06 [-2.47, 2.58]	1.29	0.96
HG:Seas:Prey	-0.14 [-2.39, 2.66]	1.28	0.92
CG:Seas:Pop	NA	NA	NA
GBB:Seas:Pop	-12.70 [-33.35, 7.95]	10.54	0.23
HG:Seas:Pop	-12.80 [-33.46, 7.85]	10.54	0.22
CG:Prey:Pop	1223 [-2217.29, 4664.02]	1755	0.49
GBB:Prey:Pop	-0.63 [-1.10, -0.15]	0.24	0.01
HG:Prey:Pop	-0.31 [-0.74, 0.12]	0.22	0.15
Seas:Prey:Pop	-0.54 [-0.72, -0.36]	0.09	<0.001
Site:CG:Seas:Prey	NA	NA	NA
Site:GBB:Seas:Prey	NA	NA	NA
Site:HG:Seas:Prey	-45.70 [-144.22, 52.83]	50.27	0.36
Site:CG:Seas:Pop	NA	NA	NA
Site:GBB:Seas:Pop	NA	NA	NA
Site:HG:Seas:Pop	14.24 [-463.39, 491.87]	243,70	0.95
Site:CG:Prey:Pop	NA	NA	NA
Site:GBB:Prey:Pop	1591 [-1868.20, 5050.97]	1765	0.37
Site:HG:Prey:Pop	959 [-2483.47, 4401.53]	1765	0.59
Site:Seas:Prey:Pop	-175.90 [-611.64, 259.82]	222.30	0.43
CG:Seas:Prey:Pop	NA	NA	NA
GBB:Seas:Prey:Pop	-0.40 [0.08, 0.72]	0.16	0.01
HG:Seas:Prey:Pop	NA	NA	NA
Site:CG:Seas:Prey:Pop	NA	NA	NA
Site:GBB:Seas:Prey:Pop	NA	NA	NA
Site:HG:Seas:Prey:Pop	NA	NA	NA

Appendix M – Manuscript of published paper

Kleptoparasitism in gulls (*Laridae*) at an urban and a coastal foraging environment: An assessment of ecological predictors.

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ABSTRACT

Capsule: Kleptoparasitism in gulls occurred at a greater rate at an urban compared with a coastal site. Population density and prey size predicted the rate of kleptoparasitism at the urban site.

Aims: To investigate and assess the ecological variables associated with kleptoparasitism among gulls at urban and rural sites.

Methods: Field observations were conducted at Brancaster (coastal rural) and Billingsgate Market (urban) to examine differences in the rate of kleptoparasitism in mixed-species flocks of gulls. Four key variables (prey size, population density, season and species) were assessed as predictors of kleptoparasitism.

Results: Generalized linear models revealed significant effects on kleptoparasitism rate of site, population density and prey size, and two-way interactions between these main terms. Population density and prey size differed significantly between sites, but population density appeared to predict the rate of kleptoparasitism.

Conclusion: Kleptoparasitism may well aid invasion and increase the range of environments a gull can tolerate by helping them meet their energy needs in novel environments where normal foraging behaviours are difficult to implement.

INTRODUCTION

Kleptoparasitism can be defined most simply as "seizing food gathered by another" (Hatch 1970) and it is a foraging strategy that can reduce the costs of searching for and procurement of food (Thompson 1986, Barnard 1990, Giraldeau & Caraco 2000, Giraldeau & Dubois 2008). Kleptoparasitism has been observed within and between species across various animal taxa (Brockmann & Barnard 1979) including insects (Erlandsson 1988), spiders (Coyle *et al.* 1991), mammals (Höner *et al.* 2002), and even humans (Schoe *et al.* 2009). Birds, more than other taxa, have been the focus of detailed research in this area (Barnard 1990). In a seminal and exhaustive review of the avian literature, Brockmann & Barnard (1979) identified gulls *Laridae* as the most prevalent kleptoparasites and listed ecological factors conducive to kleptoparasitism. These included large concentrations of hosts (victims) and quantities of food, and large, high quality food items to steal. Here, we focus on kleptoparasitism within and between gull species in two distinct ecologies.

Research on gulls has demonstrated that kleptoparasitism is a facultative behavioural strategy that is applied flexibly as ecological conditions vary. Field research conducted by Maniscalco & Ostrand (1997) found that the degree of kleptoparasitism co-varies with the concentration of hosts. In mixed-species foraging flocks of seabirds the rate of kleptoparasitism committed by gulls increased as the density of birds increased. The distribution of food resources covaried with foraging flock density, such that food distribution should directly predict rates of kleptoparasitism.

Hamilton (2002) explored the relationship between food availability and kleptoparasitism by assessing the distribution of foragers between patches that were high or low in the rate of food input. The model showed that less kleptoparasitism occurred in high resource input patches and that kleptoparasitism increased with decreasing resource input. Increasing the density of competitors in a patch had the effect of increasing the proportion of kleptoparasites, in line with the observations of Maniscalco & Ostrand (1997). Increasing the number of competitors and decreasing resources increased the intensity of resource competition, thus promoting kleptoparasitism.

The findings of Maniscalco & Ostrand (1997) and Hamilton (2002) strongly indicate that kleptoparasitism is a flexible behavioural strategy. However, no research has yet investigated the value of kleptoparasitism in evolutionarily novel environments. The increasing urbanisation of gull populations provides an opportunity to address this question. Many gull species that are found in urban settings are of conservation concern due to declining populations over the last 25 years or more (Eaton *et al.* 2015).

Understanding the behavioural strategies adopted by these species will help to further understand the stresses they face (Eaton *et al.* 2015, Reid 2004, Madden & Newton 2004).

Gulls are found in a variety of habitats (Pons *et al.* 2005) and have been noted for their tendency to colonise novel environments (Rock 2005). As members of the sub-order *Charadrii* they are part of only two groups of modern birds known to have been present since the Cretaceous period over 65 million years ago (Proctor & Lynch 1993). Their significant investment in kleptoparasitism highlights the importance of this strategy to gull species, and suggests kleptoparasitic behaviours may have played an important role in aiding the radiation and longevity of this family. For any animal, invading an urban environment entails finding solutions to a number of survival problems, the most pressing of which is acquiring food. Kleptoparasitism is a foraging strategy that can be used by gulls when very few conditions are met. The only essential conditions are the availability of opportunistic food sources and the presence of other foragers, of any species, to provide cues as to the location of food.

In this study, we investigated the predictors of the rate of kleptoparasitism in foraging gull populations across two environments with contrasting parameters: 1) a coastal environment, assumed to be typical of the shoreline foraging ecologies encountered by gulls throughout much of their evolutionary history and 2) an urban environment. Our predictions were: 1) that population density would be positively related to the rate of kleptoparasitism, 2) that large prey items would be more susceptible to theft, so that prey size should covary with kleptoparasitism rate, 3) that kleptoparasitism would vary between breeding (March to August) and non-breeding seasons, 4) that gull species would differ in their use of kleptoparasitic behaviour and 5) that there would be a higher rate of kleptoparasitism at the urban site, where food was predicted to be a rapidly decreasing resource.

METHODS

Study Sites

Research was conducted at two sites in the UK, between July 2014 and June 2015. Three days of observations were conducted at each site in all calendar months. Site 1 was Brancaster Beach, Norfolk, UK (52°58'30"N 0°38'11"E); a public beach situated within a saltmarsh environment, managed by the National Trust. The low tide at Brancaster exposes a large area of sand beach where numerous bird species forage for prey items exposed by the receding tide. The study area was a section of beach demarcated by two water channels where the outflow of water draining from the saltmarsh joins the sea. These two channels marked the eastern and western boundaries of the study area. At its maximum, when the tide was at its lowest point, the study area covered 1.6 km^2. Site 2 was an urban location at Billingsgate Market, east London (51°30'20"N 0°00'43"W); a commercial fish market. Research was conducted in a car park used by fish merchants to process and load stock onto vans, and covered an area of 0.0104 km^2. The size of study areas was calculated using scaled aerial photographs from Google Maps.

Study species

Large numbers of gulls aggregated daily to forage at both sites. At Brancaster, gulls aggregated to forage in mixed-species groups over a period of about four hours; two hours either side of the low tide mark. The most numerous gull species present at this site were Great Black-backed Gull *Larus marinus*, Herring Gull *Larus argentatus*, Black-headed Gull *Chroicocephalus ridibundus* and Common Gull *Larus canus*. These four species were the focus of research at Brancaster throughout the year. However, the numbers of Common Gulls and Black-headed Gulls were lower during the summer months as birds were mostly away breeding elsewhere. The foraging population of gulls at Brancaster had a mean daily population size of 176 (Range: 0 - 924) gulls. The daily mean number (and % of population) of each species at the site was: Herring Gull 75 (42%), Black-headed Gull 64 (37%), Common Gull 31 (18%) and Great Black-backed Gull 6 (3%).

Gulls aggregated at Billingsgate to exploit seafood waste and food leftovers discarded in the car park areas. The population consisted of Great Black-backed, Herring and Black-headed Gulls, and all three species were the focus of research. Great Black-backed and Herring Gulls were present at Billingsgate all year round, with some birds nesting on the surrounding market buildings. Black-headed Gulls were largely absent from the site between the April and July when they were away breeding elsewhere. The

foraging population at Billingsgate had a mean daily population size of 40 (Range: 24 - 79) gulls. The daily mean number (and % of population) of each species at Billingsgate was: Herring Gull 28 (70%), Black-headed Gull 7 (19%) and Great Black-backed Gull 4 (11%).

Measuring kleptoparasitism

Population size and composition were calculated using scan samples at 30 minute intervals. All attempts at kleptoparasitism, both successful and unsuccessful, were counted. Kleptoparasitic behaviours included the use of force to take items from another bird, theft without any interaction with the host and simultaneous theft (or attempted theft) from a host, by two or more competitors (Giraldeau & Caraco 2000). Size of food items was estimated visually in relation to bill lengths. The Herring Gull bill length was used as a standard comparative measurement to assess the length of food items (Table 1). Food items contested by the smaller or larger species of gulls were calibrated in relation to the mean size of Herring Gull bills. Prey sizes were assigned to increasingly large categories in relation to Herring Gull bill size (0.5, 0.75, 1, 2, 3, 4, 5 or 6).

[INSERT TABLE 1 ABOUT HERE]

Field observations

Brancaster: The majority of field sessions were conducted at low tide to coincide with the presence of the largest numbers of birds. Field sessions had a mean duration of 120 minutes (range: 90 – 220 minutes) and a total of 74 hours 28 minutes of observations were conducted at Brancaster over 34 days. Field sessions were conducted during daylight between 04:45 hours and 17:00 hours, to permit behaviour to be recorded on video.

An observer (RS) scanned the beach for gulls, using binoculars, and then approaching to within a distance from which foraging patches could be identified, the gulls counted and their foraging behaviour recorded on video. Patches were classified as discrete clusters of two or more birds exploiting a food source or searching for food in a given area. The location of patches was constantly shifting around the beach. Once a patch was identified, video recording was carried out from a fixed position with a Sony 8.9 megapixel HD camcorder mounted on a tripod. The distance from which a patch was filmed varied and was contingent on how closely the researcher could approach without

disrupting the foraging birds. Recording of a patch was concluded when the gulls in that patch dispersed. The duration of recordings ranged from 32 seconds to 40 minutes 47 seconds, and 142 patches were recorded in total. Videos were analysed at a later date for incidents of kleptoparasitism.

Gull counts were conducted every 30 minutes from the start of a field session, using a series of digital images (Nikon Coolpix P510 42x zoom) taken to record all gulls in the study area. These images were analysed at a later date to calculate the population size and composition.

Billingsgate: Observations at Billingsgate were conducted between 07:00 hours and 15:00 hours. The trading hours for the market were 03:00 hours to 08:30 hours. After 08:30 hours, the main activity at the site is the clean-up of the market and car park. Prior to 07:00 hours it was not possible to conduct observations due to the large number of vehicles at the site. Field sessions were conducted on days when the market was operational (Tuesday to Saturday) and when it was closed (Sunday and Monday).

Observations and recordings were conducted from a vehicle placed to give the best vantage point on the day and the position varied between observation days. Gull activity at foraging patches was video recorded by the observer (RS) until the resource in the patch had depleted and the birds dispersed. Over the study, 183 foraging patches were recorded and these ranged in duration from 25 seconds to 29 minutes 36 seconds. For each recording we noted the number of each species and ages of the gulls present. Patch videos were analysed at a later date for incidents of kleptoparasitism.

Gull counts were conducted at 30 minute intervals from the start of a field session. As at Brancaster, a series of digital images were taken of the study area, and later analysed to calculate the population at the time of the sample, including the species and ages of gulls present. The same recording and photographic equipment used at Brancaster was used at Billingsgate.

Statistical analysis

All statistical analyses were conducted using R version 3.3.1 (R Core Team, 2016). Figures were produced in R using the base package or ggplot2 version 2.1.0 (Wickham, 2009).

RESULTS

In total, there were 595 kleptoparasitic events recorded at Billingsgate and 99 at Brancaster. A single event involving a Lesser Black-backed Gull *Larus fuscus* was excluded from the analysis. There were 15 missing data points for prey size and all data associated with these observations were also removed.

Data were analysed using a series of generalized linear models (GLM). The response variable was the rate of kleptoparasitism (events per minute) for each patch observed. This variable was $\log_n$ transformed to improve the dispersion of data. The predictor variables were population density (daily mean population density (birds.km^{-2}) over each study area), prey size, season (breeding/non-breeding), species of kleptoparasite and site (Billingsgate/Brancaster). The population density, prey size and response variables were each centred and scaled in order to standardize them. Standardizing continuous variables facilitated meaningful comparisons between model coefficients. All variables were entered as main effects into a GLM using a Gaussian function with identity link (Table 2).

To avoid over-fitting a relatively small dataset, we next adopted a subtractive approach using a backward `step()` function. This is a sequential approach to model fitting using the Akaike Information Criterion corrected for finite sample sizes (AICc). Models with AICc values which differ by less than 2 are regarded as being similarly good fits, whereas differences (ΔAICc) over 2 suggest the model with the higher AICc is a poorer fit (Burnham & Anderson 2001). This approach led to the removal of season and species from the best fitting model, leaving a minimal main effects model with site, standardized population density and standardized prey size as significant predictors of kleptoparasitism rate (Table 2).

[INSERT FIGURES 1 & 2 AND TABLE 2 ABOUT HERE]

A positive correlation was apparent between population density and standardized $\log_n$ kleptoparasitism rate at Billingsgate, and to a lesser extent at Brancaster (Figure 1). A positive correlation was also seen between prey size and standardized $\log_n$ kleptoparasitism rate at Billingsgate, but this correlation appears to be negative at Brancaster (Figure 2).

Owing to the trend differences noted between sites (Figures 1 and 2), a second (Gaussian) GLM was constructed which included the main effects and all pairwise

interactions between site, standardized prey size and standardized population density. This model suggested that the interactions were significant (Table 2). Notably, however, the coefficients for the main effects of site, standardized prey size and standardized population density remained approximately the same (Table 2) indicating that the data collected at Brancaster did not evidence a trend reversal.

Data from Brancaster showed a smaller range of values for prey size and population density than Billingsgate, and in the case of population density the data ranges for the two sites were non-overlapping (x axes in Figures 1 and 2, Table 3). This suggests that additional data may be needed to be collected at Brancaster (or an equivalent site) to capture the influence of these variables on kleptoparasitism across this reduced ranges. Prey sizes and population densities were both significantly greater at Billingsate (Table 3).

[INSERT TABLE 3 ABOUT HERE]

Returning to the response variable and to explore the relative importance of pairwise interactions in the interactions model we again adopted a subtractive ΔAICc approach (using the `drop1()` function). All three pairwise interactions between the three entered variables could be removed while lowering the AICc with one exception: the site × prey size interaction. Removing only this interaction from the model resulted in an increased AICc. The reasonable fit offered by models of kleptoparasitism that include interactions and the significant differences between the two key continuous predictor variables support the view that the two sites show a core ecological difference.

DISCUSSION

Our results show that rates of kleptoparasitism in gulls are affected by bird population density and prey size. While these two predictors seem to be robustly positively correlated with increased rates of kleptoparasitisim, differences between the sites in the predictors and the response variable support a more cautious interpretation. It is possible that the population density measure may under-estimate the search time entailed for would-be kleptoparasites at Brancaster, in contrast to Billingsgate.

Maniscalco & Ostrand (1997) demonstrated how a shift in the foraging conditions in a single environment resulted in an increase in kleptoparasitisic behaviour by gulls. Our results complement that finding and describe clear frequency differences between a rural and an urban site. Our study gave focus to the role that kleptoparasitism might play in helping gulls meet their energy needs when invading urban environments. Our sample size is small – one rural and one urban environment only – and so we must be cautious in generalizing any findings. However, here we consider the mechanism by which urban invasion might occur when birds initially encounter those spaces. As Marzluff *et al*. (2001) have described, the foraging environment changes on a gradient between wildland environments and heavily urbanised spaces. As a gull moves along this gradient it will encounter fewer aspects of the foraging environment with which it is familiar. At one extreme of this gradient are heavily urbanised spaces containing lots of anthropogenic novelty with few of the characteristics of a natural food web. Billingsgate is such a site, as all the food there is waste provisioned by human activities. A gull, or small founder population of gulls, invading an urban environment must either obtain food through: innovation by exploring the novel foraging space; learning what things are edible and where to find them by copying other foragers; or stealing food from other individuals.

Previous research has emphasised the importance of innovative behaviour in species that invade novel environments (Sol *et al.* 2005, Sol *et al.* 2008). Some proportion of innovators, who explore the environment, are essential in any population otherwise there would be no one to copy, however, rates of innovation in any natural population are quite low (Page 2008), making the second two options, copying or stealing, more likely for invasive gulls. Of these, copying other foragers to learn the locations of food is necessary, but stealing can be efficient as it avoids the cost of the full foraging cycle by acquiring food discovered by another's effort. To this end, we can think of stealing information and stealing food as on a continuum; the cost of stealing the food is actually the marginal cost of stealing conditional on already observing the victim.

As gulls can range over large areas they can occupy different habitats on the gradient described above in a single foraging bout or day. This suggests a plausible

alternative mechanism to the one described above by which gulls can invade urban spaces. They can forage in environments where they encounter conditions with which they are familiar, and then make forays and encroachments into urban spaces in search of supplemental food and other foraging populations. Foraging in the littoral zone of rivers and estuaries that pass near or through cities is an example of how this might work. In our argument regarding the utility of kleptoparasitism we have made the assumption that while this second mechanism would undoubtedly occur, the additional travel and foraging costs involved would make it energetically more expensive than exploiting other foragers through kleptoparasitism. These costs would not be prohibitive of this foraging approach but we suggest that these additional costs would make it secondary to the kleptoparasitic strategies considered above. At present little is known about the foraging habits and ranges of urban gull populations, and tracking of individuals to see the extent of their foraging ranges was not undertaken in our study. Further work of this nature would be useful to assess whether urban gull populations, such as the one at Billingsgate, obtain their food exclusively at that site or exploit a variety of habitats.

Comparing the range and diversity of environments occupied by different gull species may also provide insights into the role of kleptoparasitism in supporting invasion. As described by Brockmann & Barnard (1979) 23 of 88 gull species are reported to use kleptoparasitism. A comparison between kleptoparasitic and non-kleptoparasitic gull species of the diversity of habitats that these species routinely breed and forage in, and the extent of their ranges, may provide indirect evidence for the proposed role of kleptoparasitism as a strategy that buffers against environmental change. If this proposed function of kleptoparasitism is plausible we should expect to see kleptoparasitic gull species occupying a broader diversity of habitats than non-kleptoparasitic gull species.

Ecological predictors of kleptoparasitism

Birds are dispersed widely at Brancaster and population density was positively correlated with kleptoparasitism. This finding is consistent with empirical research that shows foragers are more likely to encounter each other at high population densities and interact aggressively (Colwell 2010). It also lends support to the theoretical model of Hamilton (2002) demonstrating increased kleptoparasitism with increasing competitor density.

In addition, King *et al.* (2009), in research on baboon troops, found that the distribution of resources influenced the rate of kleptoparasitism, with small tightly

clustered patches prompting more kleptoparasitism. The resources in the study environments at Brancaster and Billingsgate were clearly distributed in different ways that provided a useful test of the pattern of behaviour described by King *et al.* (2009). The food at Brancaster was naturally more widely dispersed throughout the environment and it was a much larger study area than Billingsgate, permitting gulls to be more spaced out whilst foraging. Our results support the finding of King *et al.* (2009) with more kleptoparasitism in high density areas where gulls were forced to forage closer together, perhaps making it easier to take advantage of opportunities to try and steal.

The finding that larger food items were more likely to be targeted for theft is in accord with the findings of several empirical studies (Hopkins & Wiley 1972, Ens & Cayford 1996, Leeman *et al.* 2001). Large prey items provide a conspicuous visual cue to the presence of food, and a large prey item requires longer handling time, which increases the likelihood that other foragers can approach and try to steal the item. Our use of an ordinal scale to measure the size of prey items in terms of bill lengths was a limitation of this study that may have resulted in a loss of additional data of value. Ordinal measures of this kind result in a lack of precision that may mask useful patterns of behaviour. A more finely grained measure would have been beneficial, but the ordinal measure of bill lengths used represented the most practical way to assess the size of food items from the observational data obtained.

Concluding remarks: Kleptoparasitism was higher in the urban environment. Large prey items that take longer to handle, and high population densities that increase competition for available resources were the critical aspects of the urban environment at Billingsgate that promoted kleptoparasitism. Kleptoparasitism may well aid invasion and increase the range of environments a gull can tolerate by helping them meet their energy needs in novel environments where normal foraging behaviours are difficult to implement.

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References

Barnard, C.J. 1990. Parasitic relationships. In C.J. Barnard & J.M. Behnke (eds.). *Parasitism and Host Behaviour* pp. 1-33. Taylor & Francis, London.

Brockmann, H.J. & Barnard, C.J. 1979. Kleptoparasitism in birds. *Animal Behaviour* **27:** 487-514.

Burnham, K.P. & Anderson, D.R. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28:** 111–119.

Cohen, J.E., Jonsson, T. & Carpenter, S.R. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences* **100:** 1781-1786.

Colwell, M.A. 2010. *Shorebird Ecology, Conservation, and Management*. University of

California Press, Berkeley, USA.

Coyle, F.A., O'Shields, T.C. & Perlmutter, D.G. 1991. Observations on the behaviour of the kleptoparasitic spider, *Mysmenopsis furtive* (Araneae, Myseminidea). *Journal of Arachnology* ***19*****:** 62-66.

Eaton, M.A., Aebischer, N.J., Brown, A.F., Hearn, R., Lock, L., Noble, D.G., Musgrave, A.J., Noble, D.G., Stroud, D. & Gregory, R.D. 2015. Birds of conservation concern 4. *British Birds* **108:** 708-746.

Ens, B.J. & Cayford, J.T. 1996. Feeding with other oystercatchers. In J.D. Goss-Custard (ed). *The Oystercatcher: From Individuals to Populations* pp. 77- 104. Oxford University Press, Oxford.

Erlandsson, A. 1988. Food sharing vs monopolising prey: a form of kleptoparasitism in Velia Caprai (Heteroptera). *Oikos* ***53*****:** 203-206.

Giraldeau, L.-A., & Dubois, F. 2008. Social foraging and the study of exploitative behaviour. *Advances in the Study of Behavior* ***38*****:** 59-104.

Giraldeau, L-A. & Caraco, T. 2000. *Social Foraging Theory*. Princeton University Press, Princeton.

Hatch, J.J. 1970. Predation and piracy by gulls at a ternery in Maine. *The Auk* ***87*****:** 244-254.

Hamilton, I.M. 2002. Kleptoparasitism and the distribution of unequal competitors. *Behavioural Ecology* **13:** 260-267.

Höner, O.P., Wachter, B., East, M.L. & Hofer, H. 2002. The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology* ***71*****:** 236–246.

Hopkins, C.D. & Wiley, R.H. 1972. Food parasitism and competition in two terns. *The Auk* **89:** 583-594.

King, A.J., Isaac, N.J.B. & Cowlishaw, G. 2009. Ecological, social and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioural Ecology* **20:** 1039-1049.

Leeman, L.W., Colwell, M.A., Leeman, T.S. & Mathis, R.L. 2001. Diets, energy intake, and kleptoparasitism of nonbreeding Long-billed Curlews in a northern California estuary. *Wilson Bulletin* **113:** 194-201.

Madden, B. and Newton, S.F. 2004. Herring Gull *Larus argentatus*. In: P.I. Mitchell, S.F. Newton, N. Ratcliffe, and T.E. Dunn, (eds.). *Seabird Populations of Britain and Ireland* pp 242-262. T. & A.D. Poyser, London.

Malling Olsen, K. & Larsson, H. 2003. *Gulls of Europe, Asia, and North America*. Chrisopher Helm, London.

Maniscalco, J.M. & Ostrand, W.D. 1997. Seabird behaviors at forage fish schools in Prince William Sound, Alaska. In *Forage Fishes in Marine Ecosystems*. *Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems*. Alaska Sea Grant College Program Report No. 97-01 pp 175-190. University of Alaska Fairbanks.

Marzluff, J.M., Bowman, R. & Donnelly, R. 2001. *Avian Ecology and Conservation in an Urbanising World*. Kluwer Academic Publishers, Norwell, USA.

Pons, J.-M., Hassanin, A. & Crochet, P.-A. 2005. Phylogenetic relationships within the *Laridae (Charadriiformes:Aves)* inferred from mitochondrial markers. *Molecular Phylogenetics and Evolution* **37:** 686-699.

Proctor, N.S. & Lynch, P.J. 1993. *Manual of Ornithology: Avian Structure and Function*. Yale, New Haven, USA.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/

Reid, J.B. 2004. Great Black-backed Gull *Larus marinus*. Pp 263-276 in Mitchell, P.I., Newton, S.F., Ratcliffe, N. and Dunn, T.E. (eds.). *Seabird Populations of Britain and Ireland*. T. & A.D. Poyser, London.

Rock, P. 2005. Urban gulls: problems and solutions, *British Birds* **98:** 338-355.

Schoe, M., De Iongh, H.H. & Croes, B.M. 2009. Humans displacing lions and stealing their food in Bénoué National Park, North Cameroon. *African Journal of Ecology* ***47*****:** 445-447.

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P. & Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Science*. **102:** 5460–5465.

Sol, D., Bacher, S., Reader, S.M. & Lefebvre, L. 2008. Brain size predicts the success of mammal species introduced into novel environments. *American Naturalist* **172**: 63–71.

Thompson, D.B.A. 1986. The economics of kleptoparasitism: optimal foraging, host and prey selection by gulls. *Animal Behaviour* ***34*****:** 1189-1205.

Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Tables

Table 1. Data used to obtain a standardised bill length measurement. Calculated by taking the mean bill length for both sexes for each species (from Malling Olsen & Larsson 2003), and then taking the mean of all four species' means. This averaging across species returned a figure of 45mm. This was closest to the bill length of Herring Gull (difference of 7mm). The Herring Gull bill length was therefore used to assess the size of food items in the field.

species	**m**ean male **bill length (mm)**	mean female **bill length (mm)**	mean **species bill length (mm)**	45mm - **s**pecies mean **bill length (mm)**
Common Gull	36.10	32.70	34.40	11
Black-headed Gull	33.60	31.60	32.60	12
Herring Gull	55.20	49.70	52.45	-7
Great Black-backed Gull	63.10	57.60	60.35	-15

Table 2. Summary of generalised linear models exploring the effects on $\log_n$ kleptoparasitism rate (events per minute) of site (with Billingsgate as reference), standardised population density, standardised prey size, species of kleptoparasite and season.

Model	terms	coefficients	AICc	ΔAICc
a. Main effects model	all		1474.182	6.687
b. Minimal main effects model	site	−0.86128	1468.817	1.322
	population density	+0.45983		
	prey size	+0.08091		
c. Interactions model (two-way interactions)	site	−1.35673	1467.495	0
	population density	+0.43881		
	prey size	+0.08240		

Table 3. Differences in prey size and population density between Billingsgate (N = 593) and Brancaster (N = 86). Differences between site were tested using Mann-Whitney tests.

Site	median	range	statistic
a) Population density (birds.km^{-2})			
Billingsgate	1.730	0.380 - 4.330	U = 50998, *P* < 0.0001
Brancaster	0.0190	0.0025 - 0.1250	
b) Prey size (bill lengths)			
Billingsgate	8.00	0.75 - 20.00	U = 46575, *P* < 0.0001
Brancaster	0.75	0.50 - 6.00	

Figure Legends

Figure 1. Population density plotted against standardized $\log_n$ kleptoparasitism rate at both sites, with fitted regression line and shading indicating 95% confidence intervals.

Figure 2. Prey size plotted against standardized $\log_n$ kleptoparasitism rate at both sites, with fitted regression line and shading indicating 95% confidence intervals.

Appendix N – Colour-ringed birds recorded at Billingsgate

Figure N1. Colour- ringed Herring gull (*Larus argentatus*) (S6GT) recorded foraging at the Billingsgate study site.

Figure N2. Colour- ringed Black-headed gull (*Chroicocephalus ridibundus*) (TNYL) recorded foraging at the Billingsgate study site.

Figure N3. Colour-ringed Black-headed gull (*Chroicocephalus ridibundus*) (ENA1) recorded foraging at the Billingsgate study site.